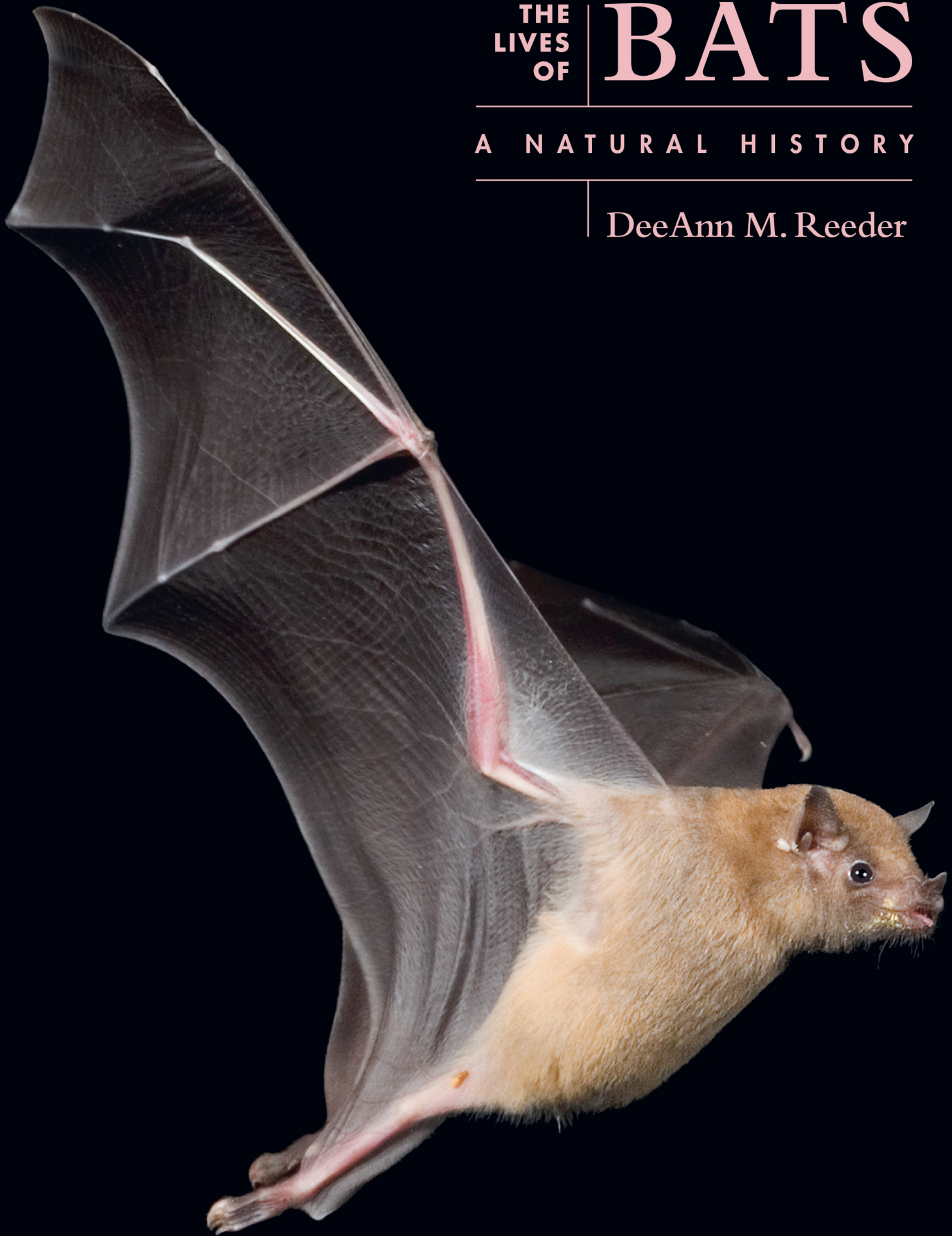
THE LIVES OF BATS

A NATURAL HISTORY

DeeAnn M. Reeder



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INTRODUCTION

The world of bats

By the end of this book, or even by the end of this introduction, I hope to have convinced you that bats are amazing creatures. As the only mammals with powered flight, they are physiologically, ecologically, and behaviorally unique. Found everywhere but Antarctica, one out of every five mammal species is a bat. This book will astound you with details of their biology, appearance, and place in the natural world.

I've never met a bat I didn't love. It's true! Even those with "interesting" appearances, such as the Wrinkle-faced Central American Bat (*Centurio senex*) on page 185, have found a way into my heart and my academic life. I have been privileged to study bats around the world and to share my knowledge of them with others. Since bats are nocturnal and fast fliers, people are not able to experience and appreciate them as they might birds or other animal groups. But bats are everywhere if you know where to look, especially if you pay attention to the night sky at dusk.

Children, if they haven't already been exposed to negative views of bats, are fascinated by them and love to learn about echolocation with modified games of Marco Polo. They also intuitively understand the ecosystem services provided by bats, which gobble up agricultural pests like moths and distribute seeds some distance from where the fruit was eaten. Nearly all bats echolocate, navigating and finding food by listening to the complex echoes of their calls. The only bat lineage without laryngeal echolocation (echolocation based upon the emittance of sounds generated in the larynx or "voice box"), the pteropodid fruit bats, consumes prey that does not give chase and is better located with their sense of smell and memory of fruiting trees. Echolocating bats can detect objects as fine as a human hair and studies of their neural processing abilities have enhanced our own use of radar. Despite persistent myths about bats, they are not blind and their navigation is aided by excellent night vision.

↓→ Most pteropodid fruit bats, like the Indonesian Short-nosed Fruit Bat (*Cynopterus titthaecheilus*), below, do not echolocate. All other bats, like Davy's Naked-backed Bat (*Pteronotus davyi*) on the right, are echolocation champions.

← Mist nets are a safe and effective way to capture bats, like this Indonesian Short-nosed Fruit Bat in flight.

→ Some researchers mark bats with numbered bands. Future recapture of these Geoffroy's Myotis (*Myotis emarginatus*) elsewhere in the range of this species will provide useful information.

CAPTURING BATS FOR STUDY

The extraordinary navigational skills of bats can sometimes make them hard to catch, as any bat biologist will tell you. Bats are usually captured for study through one of three means: direct collection from a roost (easiest with hibernating bats) using either gloved hands or a small hand net; mist-netting, similar to how birds are captured; and harp-trapping, which uses a unique contraption created solely for the purpose of collecting bats. In some locations, particularly in the tropics or outside of roosts with large numbers of bats (like caves), a mist net (which is like a giant hairnet with thin soft strings) will catch too many bats at once, a challenge for both bats and bat handlers. Certain bats, especially gleaners with the ability to hover, are exceptionally good at detecting and avoiding the nets.

With a harp trap, bats are not entangled in a net but rather fall gently into a canvas bag underneath, typically supplied with roosting materials. Dozens of bats can be captured at a time and then handled in turn with significantly less stress. Harp traps are so named because they resemble two to four musical harps set side by side, except the harps are aluminum frames from which very thin monofilament or fishing line is strung like the strings on a harp. Bats fly through the first set of strings by tucking in their wings at the last minute, but then fail to negotiate the subsequent strings on the additional panel of monofilament. After a gentle bounce on these strings, they flutter down into the collection bag and cluster with other captured bats. Depending on the study objectives, bats are then identified to species, weighed, have bone length measurements taken, and may be fitted with a band or ring on their forearm to identify them when they are captured again.

BAT EVOLUTION

I am often asked how many bats there are. As this book goes to press, 1,482 species of bats are recognized worldwide. How many individuals there are per species is not always known, but some species number in the millions. Thus, there are feasibly over 1 billion bats alive in the world today—making it possible to spot them in the sky, if not at a zoo near you. All bats are in the order

Chiroptera, from the Greek *chiro* (meaning "hand") and *ptera* (meaning "wing"), reflecting the transformation from a mammalian hand to a long-fingered wing that occurs during embryonic development. Chiroptera is the second largest order of mammals (the largest is Rodentia). In addition to wings, bats display the typical mammalian characteristics of live birth, fur, and the nourishment of young with milk. Like nearly all other mammals, they also have heterodont teeth, meaning that their teeth are not all the same. With incisors, canine teeth, premolars, and molars, each different tooth type has its own purpose. No other group of mammals displays a similar variation in feeding ecology, which has driven evolutionary diversification within bats.

Modern molecular analysis of DNA sequences from bats strongly supports the monophyly of bats, meaning that they evolved once from a single ancestor. Laryngeal echolocation evolved once and was then lost in the pteropodid fruit bats. Prior to the advent of DNA analysis, some researchers speculated that bats evolved twice and that the pteropodid fruit bats (sometimes called "megabats") were more closely related to primates based upon some shared characteristics. Even after the monophyly of bats was fully accepted, the pteropodid fruit bats were placed in the suborder Megachiroptera and all other bats in the suborder Microchiroptera. Although one still sees this terminology occasionally, we now know that some of the "microbats" are more closely related to the "megabats" than to other "microbats." In fact, both the smallest bat, the Hog-nosed Bat (*Craseonycteris thonglongyai*, page 268) from Thailand, which weighs in at approximately 0.035 oz (2 g), and the biggest bat, the Large Flying Fox (*Pteropus vampyrus*, page 238) at 2.6 lb (1.2 kg), which has a wingspan of nearly 6 ft (1.8 m), are in the suborder Yinpterochiroptera. The name of this and the second suborder, Yangochiroptera, derived etymologically from the Chinese philosophical terms "yin" and "yang," are auspicious given the Chinese cultural view of bats as the bringers of good fortune.

↑ The Hog-nosed Bat is the smallest species in the world, but is more closely related to the Large Flying Fox than to most other small bat species.

← "Megabats," like the Large Flying Fox, were once thought to be more closely related to primates.

BAT FOSSILS

The oldest known fossil bat skeleton dates from around 52.5 million years ago in the Eocene Epoch. Discovered in 2003 in what is known as the Green River Formation in the state of Wyoming, in the United States, *Onychonycteris finneyi* has the most primitive features of any fossil bat. Prior to its discovery, a different bat from the same sediments (and thus the same timeframe), *Icaronycteris index*, represented by multiple full skeleton fossils, was believed to be the most primitive. However, *Onychonycteris*, which is larger than *Icaronycteris* and other Eocene bats, has more primitive limb proportions, and, most importantly and unusually, well-developed claws on all wing digits. The genus name *Onychonycteris* originates from the Greek *onycho* (meaning "clawed") and *nycteris* (meaning "bat"), whereas the species name *finneyi* was given in recognition of the prospector Bonnie Finney (1951–2013), who collected the original holotype (the fossil that now formally represents this species), housed in the Royal Ontario Museum in Toronto, Canada.

Onychonycteris finneyi has unusually short and broad wings—a low aspect ratio (see page 62)—and relatively short and small wingtips. In this way, its wings are similar to those of the extant (that is, still living) mouse-tailed bats (for example, see the Lesser Mouse-tailed Bat, *Rhinopoma hardwickii*, page 178), which have a flight style that alternates between fluttering and gliding. Its long hind limbs may also have supported a gliding and climbing locomotor style. As gliding has been proposed as an intermediate step in the development of the truly powered, flapping flight of bats, *O. finneyi* may represent a missing link in our understanding of the evolution of bats.

Although the fossil record lacks details of what the earliest bats looked like, bats today have varied appearances. Tied to their habitat, echolocation type, and diet, bats range in color and fur pattern, wing shape, and most especially in the appearance of their faces and their ears. Some bats that echolocate have evolved "nose leaves" that serve as megaphones for outgoing calls (that they emit through their nose) and myriad bat groups have very large and maneuverable ears, the better to hear returning echoes. Other "plain-faced" bats, like the pteropodid fruit bats, resemble dogs or foxes (with wings) and from an anthropomorphic perspective are considered quite beautiful, earning them the moniker "sky puppies."

↖ *Onychonycteris finneyi* (left) is the most primitive bat ever discovered, with claws on each wing digit. *Icaronycteris index* (right) is from the same era, but shows more advanced features. Both extinct species are readily identifiable as a bat.

HOW DO BATS SURVIVE?

Bats are highly intelligent and social creatures who learn where to forage and roost from their mothers. Many bat species have perfected the art of surviving in extreme environments where food is sometimes in short supply. Bats roost in a variety of places and can survive long winters by hibernating in cold caves. Their unique physiology, attendant to the energetic demands of being a flying mammal, may hold clues for improving human health. For example, proteins identified as being responsible for the anticoagulant nature of the saliva of Common Vampire Bats (*Desmodus rotundus*) are being studied for their potential to quickly dissolve blood clots in stroke patients. Also, lessons learned from studying the ability of the bats' antiviral immune system to control inflammation may save the lives of those infected with deadly viruses like SARS-CoV-2 and Ebola.

→ Many bat species, like these Antillean Fruit-eating Bats (*Brachyphylla cavernarum*), roost in caves, which are a safe and temperature-controlled environment.

→→ Flight is energetically expensive but has allowed bats, like this Large Slit-faced Bat (*Nycteris grandis*), to exploit new resources.

EXPLORING THE LIVES OF BATS

Chapter 1 Defining Bats answers the question "What is a bat?" by describing the evolution and development of wings and by explaining how bats evolved and diversified by exploiting dietary and roosting niches all around the world. It includes the bat family tree, or phylogenetic tree, which illustrates how the different bat groups are related to each other. *Chapter 2 Bat Anatomy* dives into bat anatomy and considers the aerodynamics of bat flight and the reasoning behind bat coloration patterns. How fast and how far bats can fly is a marvel.

Chapter 3 Echolocation explores the mysteries of echolocation, from the physics of sound to the inner workings of the bat ear and brain, to the facial and ear modifications that support echolocation, and finally the ultimate coevolutionary battle: moths versus bats. Both wing shape and echolocation are intricately tied to bat diet, the subject of *Chapter 4 Diet*. While most bats are insect eaters, the expansion of bats, especially in the New World family Phyllostomidae (the New World leaf-nosed bats), into novel dietary niches, including fruit, nectar, pollen, blood, and animal meat, furthered bat diversification. Similarly, endothermy (generating one's own body heat, typical of mammals and birds) and heterothermy (saving energy by allowing one's body temperature to fluctuate) are attributes of bats intricately tied to what they eat and where in the world they live—and this is covered in *Chapter 5 Thermoregulation*. Flight, echolocation, and being an endothermic heterotherm likely evolved in tandem over the approximately 62 million years of bat evolution (see page 23).

Chapter 6 Reproduction begins with a discussion of the myriad (and strange and wonderful) ways that bats find a mate. From singing and dancing to donning a mask, male bats have creative solutions to the perpetual challenge of attracting a female. The focus then shifts to females and their enormous babies, weighing in at up to one-third of the mother's weight at birth. Most bat species have a single pup each year, but some species twin and other species give birth more than once a year. When they do, it is possible to catch bats that are simultaneously nursing one pup while being pregnant with the next. Bats are unusual in their slow life history, with a low reproductive output and very long life spans. These features are tied to their overall health and how their immune systems function.

They are also connected to the bat's ability to host viruses that pose a spillover risk to humans (although this is rare). These topics are taken up in *Chapter 7 Immunity, Health, & Zoonoses*.

Chapter 8 Bats & Humans shares global bat myths and perceptions from throughout history to the modern day. It then discusses the significant consequences of human activities for bats, detailing the bat response to habitat loss and disturbance, urbanization, and global climate change. After discussing what to do about bats in your home and other buildings, we examine additional conservation challenges for bats, including hunting for meat and medicinal purposes along with overt persecution. With many bats imperiled and some on the brink of extinction, this final chapter concludes with some solutions and hope for the future. Transforming the global perception of bats from the negative to the positive will be key in these efforts. That you are reading this book suggests you are part of breaking this chain. As we journey through the chapters together, my aim is to dispel the myths surrounding bats and leave you with a newfound appreciation of our flying friends.

↑ Bats are often (but not always) portrayed negatively in art, as in *Fairy Hordes Attacking A Bat* by the Victorian artist John Anster Fitzgerald (1819–1906).

← Bats, including this Gambian Epauletted Fruit Bat (*Epomophorus gambianus*) mother, typically give birth to a single, large pup.

←← Moths are a favorite food of many bat species, including the Alpine Long-eared Bat (*Plecotus macrobullaris*).

DEFINING BATS

The only flying mammal

Bats are the only mammals that can truly fly, which makes them anatomically, ecologically, behaviorally, and physiologically unique. Although gliding is thought to have evolved independently in mammals at least six times, the ability to truly fly—volancy—has only evolved once.

Flight allows bats to utilize three-dimensional space in ways only rivaled in mammals by marine species. For these aerial predators and fruit eaters, access to the open sky provides unique opportunities for finding food, locating roosts and mates, exploring new areas, and escaping predators. It also allows them to travel great distances in search of new food sources or safe places to hibernate. Long-distance migration, sometimes aided by the prevailing winds, is an annual event for some species.

Despite its obvious advantages, powered flight is only believed to have evolved four times in nature. Flight evolved first in insects, about 350–400 million years ago. This novel mode of locomotion opened up new opportunities for these ancient arthropods and is largely responsible for the success of insects in nature. Estimates suggest that 90 percent of all animal species on Earth are insects.

Within vertebrate animals, powered flight evolved three times—in pterosaurs, birds, and bats (see page 24). Approximately 228 million years ago, powered flight evolved in the vertebrate lineage family line that would become the pterosaurs, named for the Greek words *pteron* (wing) and *sauros* (lizard). At their height, pterosaurs varied dramatically in size, shape, and diet, with wingspans that ranged from 10 in (25 cm) to 36 ft (11 m). They had a sizable keel on their breastbone, which provided a large surface area for muscle attachment, and a number of other skeletal modifications. Wings were formed by a single elongated digit of the hand, which connected their skin membrane to the body.

The oldest known birds, animals in the genus *Archaeopteryx*, date to around 150 million years ago. How flight arose in this dinosaur clan is unresolved, but

birds are one of the most successful vertebrate groups, with over 11,000 species alive today. Pterosaurs and birds would have overlapped in time for approximately 78 million years. Pterosaurs are believed to have died out in the Cretaceous–Paleogene extinction event, about 66 million years ago, which wiped out all non-avian dinosaurs and many other vertebrates. Terrestrial vertebrates that survived this event include the birds, reptiles and amphibians, and early forms of mammals, already divided into their three main groups: the egg-laying monotremes, the marsupials, and the "true placental" mammals—the eutherians—from which bats arose.

With the extinction of the dinosaurs, eutherian mammal diversification exploded, giving rise to many of the forms of mammals seen today. The success of these groups within the mammal family tree was likely due, at least in part, to the ability of these "true placental" mammals to nourish and protect their developing young in the womb. Current estimates based on molecular analysis of DNA sequences place the origin of bats at 62 million years ago, not long after the Cretaceous–Paleogene extinction event.

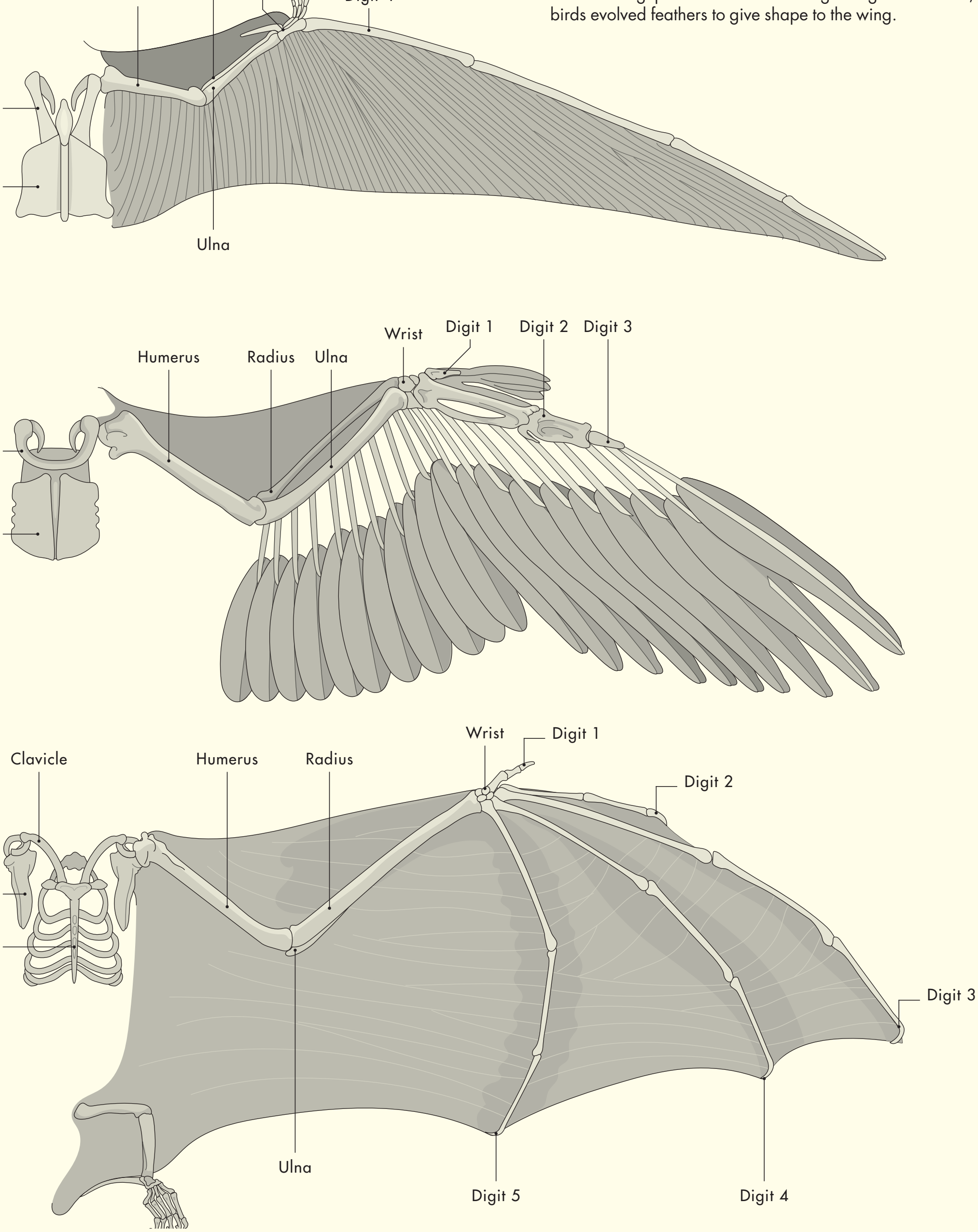
↑ (Top) The bat wing consists of an extended hand and finger with skin stretched between them, allowing for fine control when flying. (Inset) Gliding mammals, such as this Giant Flying Squirrel (*Petaurista alborufus*), with membranes between the wrist and ankle (and sometimes tail) have less control and cannot truly fly.

← Straw-colored Fruit Bats (*Eidolon helvum*) return to their roosts at dawn after flying great distances in search of ripe fruit.

CONVERGENT EVOLUTION

Wings from pterosaur, bird, and bat

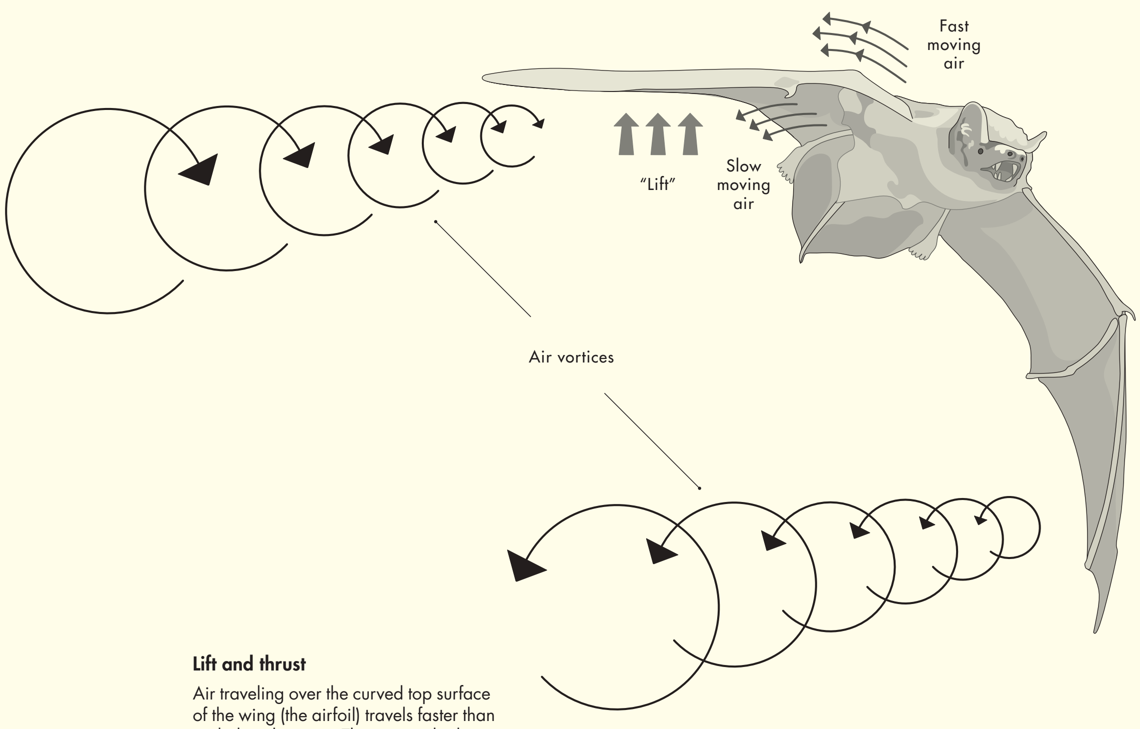
Flight evolved independently in pterosaurs (top), birds (middle), and bats (bottom). In each case, natural selection operated on the existing arm and hand to create these wings, which are similar in many ways. Robust sternums provided attachment points for the large muscles needed to power flight. Both pterosaurs and bats stretched skin over elongated finger bones (digits, labeled by number), with the wingtip at the end of their longest digit. In contrast, birds evolved feathers to give shape to the wing.



"THE HAND WING"

In contrast to the gliding mammals—enabled in most groups by a skin membrane connecting the wrist and the ankle—bats, with their "hand wing," have true powered flight. In fact, of the three vertebrate fliers, bats have much more sophisticated control over wing shape and curvature in real time. They are truly the champions of flight, with greater maneuverability than birds and pterosaurs. Nevertheless, the basics of powered flight are the same in all fliers: flight is a function of both lift and thrust. Flying requires being lifted into the air and moving forward.

Like the wing of an airplane, the bat wing has convex curvature—it forms an airfoil—which generates lift. Because of the curvature, air that passes over the top of the wing is faster than air that passes under the wing. Consequently, air pressure below the wing is higher than air pressure above the wing, which effectively pushes the wing upward. For bats, the airfoil is primarily formed by the skin membrane between the fifth finger and the bat's body, and lift is generated in the upward stroke of the wingbeat cycle. While airplane engines produce thrust, how bats produce thrust is more complicated and not fully understood. Current thought is that thrust is generated in the downward stroke of the wingbeat cycle as air moving across the top of the wing produces vortices. The rotation of the air in the space the bat just occupied produces thrust that propels the bat forward. The energy required for lift and thrust—for powered flight—comes from the extraordinary variety of dietary sources that fuel bats across the planet.



Lift and thrust

Air traveling over the curved top surface of the wing (the airfoil) travels faster than air below the wing. This creates higher air pressure below the wing, which generates lift. Air vortices created by wingbeats provide thrust, propelling the bat forward.

How hands became wings

How bats arose from small, insect-eating nocturnal mammals is a feat of evolution, which is only partially understood from the fossil record. Despite this gap in evidence, we can infer evolutionary pathways by comparatively studying bat development and bat genes.

Evolution by natural selection favors individuals with traits that help them survive and reproduce better than others. Genes are the units of heredity and variations in genes, influenced by the environment, contribute to the observable characteristics or traits of an individual, known as the phenotype. For example, if a particular variant of a gene—an allele—affects the shape of the finger bones and improves flight ability, the animal that possesses that allele may forage more effectively and survive and reproduce at higher rates than bats with a different allele. Over time, the frequency of these advantageous genes increases in a population, which drives the adaptation and evolution of species.

→ The wings of bats, like this Australian False Vampire Bat (*Macroderma gigas*), evolved over millions of years.

EVOLUTIONARY DEVELOPMENT

Evolution by natural selection sometimes occurs more rapidly than expected by acting on developmental mechanisms. Changes in the timing, sequence, or regulation of developmental events can have significant effects on an organism's phenotype. When natural selection acts on developmental processes, ancestral characters, such as the presence of a tail in mammals, are sometimes preserved in an organism's development in the womb. This is even true in humans, in which early-stage embryos display a tail similar to that of other primates. By eight weeks of development the tail has disappeared, fusing with the coccyx (tailbone). The study of how developmental characters can help us understand evolutionary relationships is abbreviated to "evo-devo."

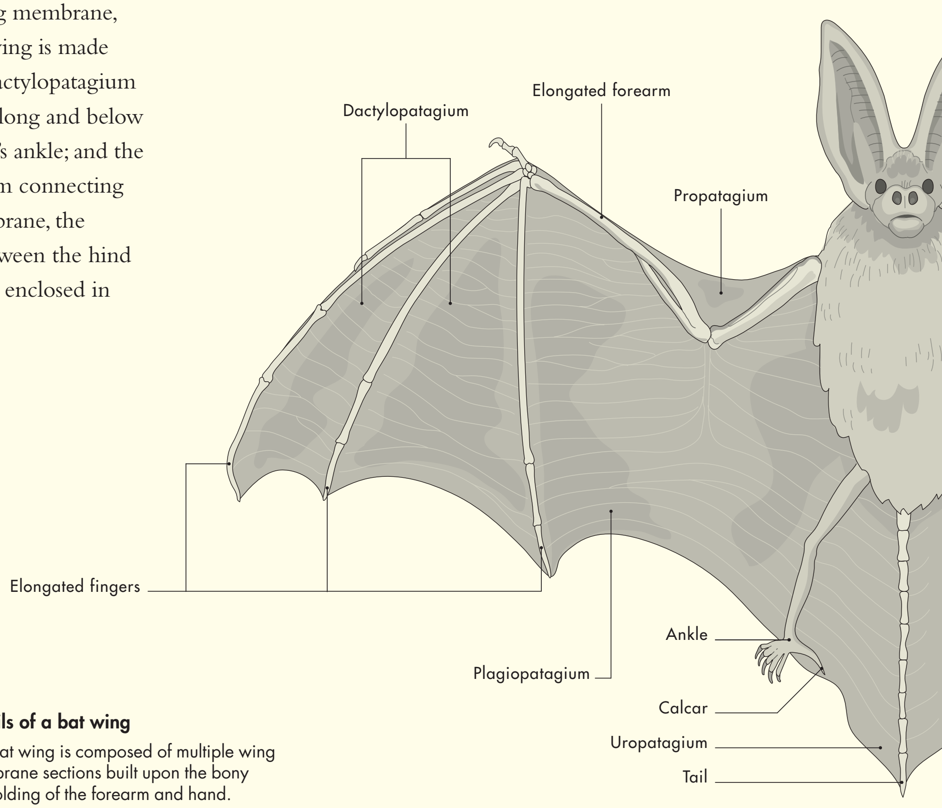
↑ Flying foxes, such as this Gray-headed species (*Pteropus poliocephalus*), do not have a tail and have only a small wing membrane between their feet (uropatagium).

THE EVOLUTION OF BATS

How did bats arise from a group of small, nocturnal, insectivorous mammals, free to conquer the night sky? Some answers to this question have been provided by the comparative study of development in the mouse and bat forelimb. At the early stages, as the cartilage template is formed, mouse and bat forelimbs are similar in size. However, as cells proliferate, differential elongation of the digits and the long bones of the bat forelimb soon become apparent. Differences in the growth rates of these bones during development partly explain the differences in bone proportions in different bat species. For example, bent-wing bats, such as Schreibers's Long-fingered Bat (*Miniopterus schreibersii*, page 42), have elongated middle finger bones, resulting in long, narrow wings and fast flight. A number of different genes appear to be responsible for turning on this growth in the digits at different times and rates than in other mammals.

This elongated forearm and fingers provide the scaffold for the strong yet elastic bat wing membrane, which forms at the same time. The bat wing is made of up three individual membranes: the dactylopatagium between the digits; the plagiopatagium along and below the forearm to the fifth digit and the bat's ankle; and the propatagium along and above the forearm connecting the wrist to the shoulder. A fourth membrane, the uropatagium, is present in most bats, between the hind limbs. The bat tail, if present, can be fully enclosed in the uropatagium or may emerge from it.

Of these four wing membranes in bats, only the dactylopatagium has a shared evolutionary origin with other mammals. During early embryonic development in mammals, a web of skin exists between the growing digits of the hands and feet. In most mammals, like mice, the cells that make up these webs of skin die off, resulting in separation of the fingers and toes. In bats, this process only occurs in the hind feet, leaving a web of skin between the fingers. The plagiopatagium, one of the three novel wing membranes in bats, arises in utero from outgrowths of skin on the side of the body. The origins of the remaining two wing membranes are unclear, but likely similar. No matter how they develop, that all four membranes are advantageous to bats and would have been under selection is clear, especially for the plagiopatagium, which forms much of the airfoil needed for producing lift during flight.



Details of a bat wing

The bat wing is composed of multiple wing membrane sections built upon the bony scaffolding of the forearm and hand.

Masters of the night sky

Bats play many different roles in ecosystems around the world. These roles are called niches, a concept that encompasses the resources bats utilize, the interactions they have with other species, and the way they respond to their environment. Bats evolved to fill a niche not exploited by others—hunting in the sky at night.

At pivotal times in evolutionary history, vacant or unoccupied niches have provided new opportunities for evolving organisms. For bats, some 62 million years ago, the initial opportunity was nighttime flying insects—a food resource exploited by few others. As bats took to the sky, aided by ever improving wings and other anatomical and physiological features, they became specialized and diversified into multiple lineages, each species with its own niche. Most of this diversification centers around bat diet. The ancestor to early bats was most likely a small non-flying insectivore.

Fossil bat teeth and inferences from the bat family tree indicate that the earliest bats were also insect eaters. Most modern bats are still insect eaters. While some are generalists and eat many different types of insects, many are highly specialized to hunt and to consume specific types of insects, such as hard-bodied beetles, moths, or even scorpions.

Once bats had mastered the night sky, additional dietary niche opportunities were presented. The ability to survive on plant-based resources, such as fruit, nectar, pollen, and occasionally leaves, evolved independently in multiple bat lineages. Similarly, over time, natural selection favored bats with increasing skills in hunting other vertebrates. Some bats today, like the Greater Bulldog Bat (*Noctilio leporinus*, page 46), with its enormous feet, are experts at catching fish. Other species specialize in hunting birds, lizards, or small rodents. Still others, the three species of vampire bats (family Phyllostomidae), exploit the niche of blood as a food resource.

← The Variegated Butterfly Bat (*Glauconycteris variegata*) often feeds over water, consuming insects like mosquitos as they emerge. It also scoops water into its mouth to drink while flying.

↑ Some bats, like the Egyptian Slit-faced Bat (*Nycteris thebaica*), hunt by gleaning prey from the forest floor.

Biogeography, roosts, and bat diversification

The evolution of bats over the past 62 million years occurred in a globally changing world in which climate, elevation, and food sources varied over time and space. The number of bat species, a metric of biodiversity, is greatest in tropical environments near the equator, especially in South America with its different elevational niches. Diversity is lowest in desert regions, polar regions, and very high mountain ranges where roosts and food are in short supply.

During the Early Eocene, roughly 55 to 47.5 million years ago, bats appear in the fossil record nearly simultaneously in North America, South America, Europe, India, and Australia. The lack of fossils from the approximately 10 million years between when molecular analyses suggest bats arose and when fossils first appeared leaves many unanswered questions about when and where bats evolved.

What is clear is that during the past 62 million years, bats have found their way to nearly every place on Earth. Although bats are not currently present in Antarctica due to the extreme cold and a lack of suitable roosts or food, fossil bats may eventually be found there as Antarctica was once much warmer and,

← The aptly named Northern Bat lives north of the Arctic circle and thus has adapted to extreme variation in daylight and temperature patterns.

↗ New World leaf-nosed bats have exploited many food niches. This Honduran White Bat (*Ectophylla alba*) is one of the smallest fruit-eating bats.

until approximately 30 million years ago, connected to South America. Some bats thrive to this day near the opposite pole, well north of the Arctic Circle. The Northern Bat (*Cnephaeus nilssonii*, page 48) thrives in the land of the midnight sun.

Differences in bat biodiversity by location are a function of history—that is, the bat lineages that arose in which places at what time, mediated by differences in the behavioral, anatomical, and physiological adaptations to changing environments. For example, in the New World tropics, nose-leaf bats in the family Phyllostomidae underwent significant and rapid diversification, resulting in the greatest diversity of foraging strategies among bats. This was enabled by the wide availability of different dietary niches, including those created by the explosive diversification of the angiosperms (plants that produce flowers and fruit). Although well adapted to the tropical regions of the New World, phyllostomid bats are replaced in temperate North America by bats in the family Vespertilionidae, champions of hibernation. In contrast to families like the Phyllostomidae, which experienced major diversification, some bat families are significantly geographically restricted, such the Mystacinidae of New Zealand, which contains only two species.

ROOSTING

Within their various habitats, the locations where bats rest, or roost, are varied and may differ by season or even within a 24-hour period. As we will see throughout this book, roosting requirements are species-specific and intricately connected to many aspects of bat biology. For example, differences in bat coloration patterns and markings are tied to the need for camouflage while roosting, mainly for those species that roost in more open environments such as along tree trunks or under leaves.

→ The Jamaican Fruit-eating Bat (*Artibeus jamaicensis*) readily roosts in man-made structures, such as the inside of this hut.

↓ Some bat species, such as these gregarious Little Red Flying Foxes (*Pteropus scapulatus*), roost in large groups in trees.

Roosts must also meet a bat's thermoregulatory needs, being either cold in winter to support the energetic savings of hibernation or warm in summer to support growing bat pups. Bats often select roosts based on the specific microclimate (temperature and humidity) they provide. This is especially true for bats that roost in enclosed environments such as caves, hollow trees, and rock crevices. Sometimes multiple bat species cluster together in the same roost. For the same thermoregulatory reasons, or perhaps simply out of convenience, bats occasionally roost in one location during the day and take their shorter nighttime rest (between feedings at dusk and again at dawn) in a different location.

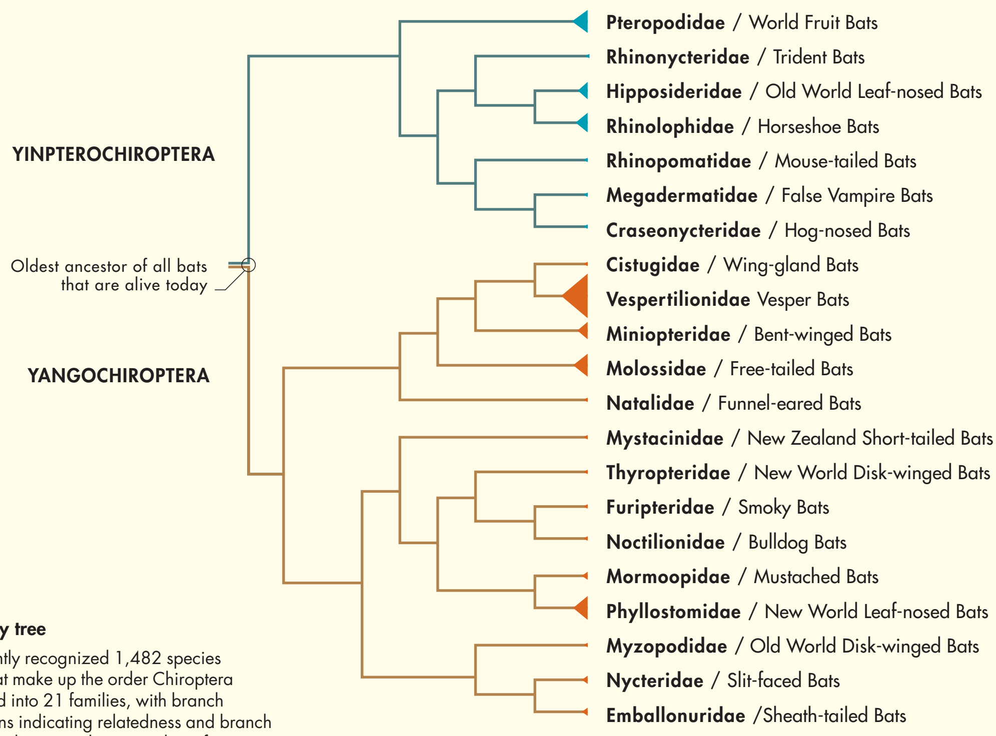
Many bat species that roost in closed-in spaces are also perfectly happy to make a home in human-made structures if they meet their needs. Mines and old railway tunnels are favorites for hibernating bats, especially if they are abandoned. Similarly, under bridges, barns, attics, church steeples, or even wooden house shutters often create just the right conditions for bats in summer, especially older structures with rough-cut wood and hiding places within the frame. The Jamaican Fruit-eating Bat (*Artibeus jamaicensis*), for example, will readily roost in various buildings. As many bats now find their previously pristine habitats converted to urban centers or farms, human-made roosts, including bat houses, may provide the missing roosts necessary for continued survival. Bats that have adapted to roosting in human-made structures or in urbanized environments are called synanthropic, from the Greek *syn* (with) and *anthropos* (man).

Understanding bat taxonomy

Bats are often considered "mice with wings," epitomized by the German moniker *Fledermaus* (fluttering mouse). Nothing could be further from the truth, as bats are only distantly related to rodents and are nested instead in the mammal family tree among the shrews, carnivores and pangolins, hooved mammals, and whales. This unique group, united by DNA and not anatomical similarity, evolved in the northern supercontinent of Laurasia around 100 million years ago.

Our understanding of how organisms are classified has evolved over time. The modern system of assigning species a Latin binomial name, consisting of a genus name and a species epithet (like *Homo sapiens*), was codified by Carl Linnaeus in 1758. A given species, such as Geoffroy's Trident Leaf-nosed Bat (*Asellia tridens*), is referred to by both its genus and species epithets, which are always italicized. Scientific names are occasionally drawn from an important location or scientific figure, but are typically a Latin derivation of some description of the organism's appearance or biology. For example, in the Latin name for the Indiana Myotis (*Myotis sodalis*, page 50), *Myotis* means "mouse-eared." This bat's specific epithet, *sodalis*, means "comrade" because it is very similar in appearance to—and occasionally co-roosts with—the once more common Little Brown Myotis (*Myotis lucifugus*).

← Geoffroy's Trident Leaf-nosed Bat is one of the 92 bat species in the family Hipposideridae.



Bat family tree

The currently recognized 1,482 species of bats that make up the order Chiroptera are placed into 21 families, with branch connections indicating relatedness and branch tip width indicating relative number of species. These families fall under two suborders, Yinpterochiroptera and Yangochiroptera, which diverged from each other circa 62 million years ago (see page 278).

Standardization of species names helps us understand biodiversity and facilitates research and conservation. All bat species today also have one or more common names, sometimes in different languages.

The 1,482 currently living species of bats can be distinguished from one another through a suite of different characters, including morphological differences, ecological niche, differences in echolocation calls, and relatedness as determined through DNA analysis. New species continue to be discovered and scientists sometimes find that what was once considered a single bat species may contain more than one taxon.

When classifying organisms within an evolutionary framework, a discipline called systematics, a genus represents a group of closely related species. Related genera are placed within families, 21 of which are recognized today within the living members of the order Chiroptera. Within this system of orders, families, genera, and species, additional subcategorization is sometimes used to reflect evolutionary divergences where known. Two suborders are recognized in Chiroptera: Yinpterochiroptera and Yangochiroptera. These two bat lineages diverged very early within the rapidly evolving bat ancestor. Graphical representation of the evolutionary relationships between organisms that include the branching points where lineages, such as Yinpterochiroptera and Yangochiroptera, diverged from one another are called phylogenetic trees, which indicate either evolutionary time or genetic distances across lineages by the length of their branches.

↑ Rendall's Serotine (*Pseudoromicia rendalli*), in the family Vespertilionidae, is an echolocating insect eater like the ancestral bat and most bat species alive today.

↗ The Indian Flying Fox (*Pteropus medius*), in the family Pteropodidae, does not echolocate but rather uses vision and sense of smell to locate fruit, flowers, and leaves.

BATS IN CLOSE-UP

Within the mammal phylogenetic tree, bats represent a single branch—they are monophyletic, meaning that there is a single evolutionary origin for all bats. Molecular data place the bat branch firmly within another monophyletic clade, the Laurasiatheria, which includes such strange bedfellows as the shrews and moles, carnivores and pangolins, and the hooved mammals and their descendants (whales!). The divergence of the ancestral Laurasiatheria and its sister group, the ancestral Euarchontoglires, from which the rodents arose, is estimated to have occurred nearly 100 million years ago. Bats are most definitely not flying mice.

How the diverse array of bats are related to one another, and which groups contain the most diversity, is evident from the phylogenetic tree of all 21 living families. Vespertilionidae is the most specious family, with 533 species found worldwide. With the exception of a few carnivorous species, bats in this family eat insects. The next largest family is the Phyllostomidae, a New World family with 230 species that is well studied for its extreme dietary diversification. The Old World fruit bats in the family Pteropodidae, sometimes called "megabats," constitute the next largest group, with 202 species. Relatively large, with simple faces that resemble dogs or foxes, species in this family do not produce ultrasonic echolocation calls. In contrast to these large families, a number of bat families are exceptionally small. In fact, one bat family, the Craseonycteridae, is monotypic, containing only the tiny Hog-nosed Bat, which was discovered in Thailand in 1973. Six additional families are also less diverse, with only two species each.

↑ A close-up of Wright's Happy Tube-nosed Fruit Bat (*Nyctimene wrightae*) shows the unusually shaped nostrils that define this group of bats.

↑ Tube-nosed Bats, such as this Queensland Tube-nosed Fruit Bat (*Nyctimene robinsoni*), can detect odors in each nostril separately while in flight, which helps them localize ripe fruit.

↑ Keast's Tube-nosed Fruit Bat (*Nyctimene keasti*) is readily identified by its bright yellow spots. Known only from three Indonesian islands, it is threatened by habitat loss.

MINIOPTERUS SCHREIBERSII

Schreibers's Long-fingered Bat

Long narrow wings

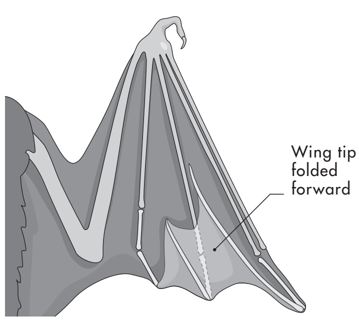
SCIENTIFIC NAME	*Miniopterus schreibersii*
FAMILY	Miniopteridae
DIET	Moths
HABITAT	Varied, semidesert steppes, Mediterranean scrub and forests
CONSERVATION STATUS	Vulnerable
WEIGHT	0.35–0.49 oz (10–14 g)
WINGSPAN	12 in (30 cm)

Schreibers's Long-fingered Bats are one of 41 species in the Old World family Miniopteridae, unique in their ability to fold back an exceptionally long third finger when not flying. As aerial hawkers, they hunt for flying insects, specializing in moths.

Long-fingered Bats, sometimes also called "Bent-wing Bats," are small to medium-sized bats with a simple muzzle, a tail enclosed in the wing membrane that stretches between the legs, and an extremely elongated third finger. This elongation, due to significant lengthening of the second phalanx of the third digit, results in some of the longest and narrowest wings within bats, supporting long-distance flight in open environments.

This species changes roosts several times per year and may migrate hundreds of miles. Schreibers's Long-fingered Bat was once thought to be widespread across Africa, Asia, and Australia. However, recent molecular studies have demonstrated that what was once considered *Miniopterus schreibersii* actually contains at least 11 different bent-wing bat species. This taxonomic splitting has refined our understanding of which bats from which locations are truly *M. schreibersii*, restricting it now to southwestern Europe and North Africa through the Middle East to the Caucasus.

Across its range, populations are declining due to habitat loss and disturbance, including that from ecotourism and from improperly designed cave "gates." These barriers, with multiple small gaps, allow bat access while limiting human entry. Unfortunately, bats will sometimes abandon caves if the gap spacing creates flight challenges. In the last 20 years, a number of mortality events have occurred, with mass die-offs of thousands of bats. While most are unexplained, those in Spain and Hungary were associated with the Lloviu virus, a relative of Ebola.



Long wing
The tip of the long wing of Long-fingered Bats folds forward to tuck out of the way, making climbing easier.

→ Schreibers's Long-fingered Bats forages mainly in open areas and is protected in most of its geographic range.

ASELLIA TRIDENS

Geoffroy's Trident Leaf-nosed Bat

Largest trident leaf-nosed bat

SCIENTIFIC NAME	*Asellia tridens*
FAMILY	Hipposideridae
DIET	Beetles, moths, flies, and grasshoppers
HABITAT	Varied, mostly desert and semidesert
CONSERVATION STATUS	Least Concern
WEIGHT	0.21–0.46 oz (6–13 g)
WINGSPAN	Not known

Geoffroy's Trident Leaf-nosed Bat is a member of the large Old World bat family Hipposideridae, a group of bats easily distinguished by the structure of their nose leaves, their broad and mobile ears, and their constant frequency (CF) echolocation calls.

Geoffroy's Trident Leaf-nosed Bat is a very common and widely distributed species in North Africa and parts of Asia. It can be found in a variety of habitats but is mostly associated with oases and dry riverbeds of desert and semidesert habitats. This gregarious species roosts in enclosed spaces, including caves, mines, and rock caverns, but also takes advantage of human-made structures such as underground irrigation channels, buildings, cellars, temples, and tombs. Although this species may roost in small numbers, up to 5,000 individuals have been reported from a single cave in Iran. It usually only roosts with bats of the same species but has been found to occasionally co-roost with the Persian Trident Bat (*Triaenops persicus*), mouse-tailed bats (*Rhinopoma* species), and the Egyptian Rousette (*Rousettus aegyptiacus*).

The name of this lineage of bats is derived from the large and distinctive nose leaf with three subtriangular projections, which form a trident. The muzzle of Geoffroy's Trident Leaf-nosed Bat is relatively short and its fur is brownish gray; it is darker on its back than on its front. The species is highly seasonal. Females roost together in maternity colonies and each gives birth to a single pup in June or July, which it nurses for approximately 40 days. This bat migrates between the summer and winter, putting on fat in the late fall just before migration.

→ Geoffroy's Trident Leaf-nosed Bat adeptly clings to the rock ceiling of a cave. Their highly mobile ears allow them to sense their surroundings.

NOCTILIO LEPORINUS

Greater Bulldog Bat

Huge feet

SCIENTIFIC NAME	*Noctilio leporinus*
FAMILY	Noctilionidae
DIET	Fish and occasionally aquatic arthropods
HABITAT	New World tropics
CONSERVATION STATUS	Least Concern
WEIGHT	1.8–3.2 oz (50–90 g)
WINGSPAN	Around 20 in (50 cm)

The handsome Greater Bulldog Bat is a common and well-studied species found in neotropical forests, always in proximity to bodies of water. Males are typically orange or yellow and have brighter colored fur than females.

Bulldog Bats are so named due to their large, floppy lips and cheeks, dominant on faces that are otherwise plain, without nose leaves or other adornments. In support of their fish-eating habit, their hind limbs are larger than most bats, with large feet and long, curved, and very sharp claws. Although they cannot detect fish under water, as soon as a surfacing or jumping fish disturbs the water, the bat's sensitive echolocation will pick it up. When surfacing fish are very abundant, the bat switches tactics and deploys a "random rake" strategy, dragging the tips of its feet through the water for up to 3 yards (10 m). When their toes hit a fish, the claws spear the fish and close around it, aided by a scooping action performed by the uropatagium. The bat then moves its legs up and its head down, transferring the fish to its strong jaws. Larger fish are carried back to a perch for easier processing.

Female Greater Bulldog Bats give birth to a single pup each year, with the timing linked to seasons of highest food availability. Both infant and adult Greater Bulldog Bats emit an array of communication calls, mostly in the ultrasonic range (above human hearing). These capable hunters also eavesdrop on other Greater Bulldog Bats by listening for feeding buzz echolocation calls, thus learning where the best foraging opportunities are.

→ A female Greater Bulldog Bat rakes the surface of a pool of water in search of fish. Some females are paler than males.

CNEPHAEUS NILSSONII

Northern Bat

Pushes northern limits

SCIENTIFIC NAME	*Cnephaeus nilssonii*
FAMILY	Vespertilionidae
DIET	Insectivorous, primarily small Diptera
HABITAT	Varied, including boreal and high mountain forests
CONSERVATION STATUS	Least Concern
WEIGHT	0.3–0.46 oz (9–13 g)
WINGSPAN	9.4–11.0 in (24–28 cm)

The Northern Bat is a fast-flying and widely distributed insectivorous species found in a diversity of habitats across the northern regions of Eurasia. Highly adaptable, it even lives north of the Arctic Circle in Norway, Sweden, and Finland.

The most northerly distributed bat, the Northern Bat is known for its long, luxurious, silky, and shaggy fur, which is dark brown to black with frosted gold-yellow tips on the back and lighter brown or beige fur on the front. Its ears and tragus (a cartilaginous projection at the base of the ear that plays a role in echolocation) are short and rounded. Like all bats in the family Vespertilionidae, their faces are plain, without any fleshy appendages or features. Their fast flight is supported by broad and long wings, and they hunt in open woodlands or forest edges. Naturally a tree-cavity and cave-roosting species, the Northern Bat readily adapts to human-made roosts, including houses and cellars. It is a frequent visitor to city parks and gardens. Although the Northern Bat will consume beetles and moths, its primary food sources are small Diptera, which include mosquitos, midges, and gnats.

Like other hibernating temperate species, female Northern Bats form maternity colonies, groups of reproductive females that roost together and give birth at roughly the same time in the summer. Females establish and defend small feeding territories that have abundant insects. Northern Bats in their highest ranges are faced with continuous midsummer daylight. Under these conditions, one might expect them to hunt during daytime hours when insects are more plentiful. However, bats feed primarily between 11 p.m. and 7 a.m., following their normal patterns in other locations.

→ The Northern Bat, with its distinctive fur, can sometimes be found roosting in and on human-made structures, like this concrete wall.

MYOTIS SODALIS

Indiana Myotis

A picky rooster

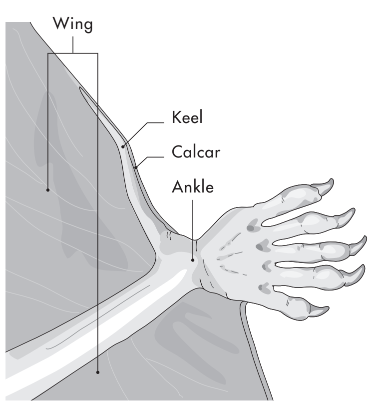
SCIENTIFIC NAME	*Myotis sodalis*
FAMILY	Vespertilionidae
DIET	Varied insects, including moths and Diptera
HABITAT	Wooded or semi-wooded upland forests
CONSERVATION STATUS	Endangered and declining
WEIGHT	0.18–0.35 oz (5–10 g)
WINGSPAN	9.4–10.6 in (24–27 cm)

This bat species, first described from Indiana, in the United States, is listed as "Near Threatened" by the International Union for the Conservation of Nature (IUCN) but "Endangered" by the US Endangered Species Act.

Indiana Myotis, a hibernating species, is found in forested areas in the eastern half of the United States. In both summer and winter, it has specific roosting requirements. Small groups of females form maternity colonies and each gives birth to a single pup in hollow dead trees or under the loose bark of dead or living trees. In the winter, both sexes hibernate in the coldest and most humid caves.

Approximately 85 percent of the total population hibernate in just nine sites. Such specific preferences place this species at risk when habitat loss and degradation, forest fragmentation, and winter cave disturbance occur. Urbanization and development have thus historically posed the greatest risk to this species. Since being listed as Endangered in the United States, populations have declined by 50 percent. Part of this decline is due to their susceptibility to the fungal pathogen that causes White-nose Syndrome (see page 222).

Light to grayish brown in color and with soft, dull fur, Indiana Myotis can be difficult to tell apart from the Little Brown Myotis (*Myotis lucifugus*), with which it shares much of its range. Careful examination distinguishes the Indiana Myotis by the presence of a keel, or bump, on the calcar. The presence of shorter hairs on the toes relative to Little Brown Myotis is also diagnostic, as is the pinkish-colored nose.



Cartilage spur

Most bats have a calcar, a spur of cartilage that connects to the ankle and helps to support the wing. The Indiana Myotis has a bump or keel on the calcar not present in the Little Brown Myotis.

→ The Indiana Myotis migrates between its summer roosts, in which it forms maternity colonies, and the caves in which they hibernate.

BAT ANATOMY

The bat body

The bat body is a marvel of evolution, built to support powered flight in a uniquely mammalian way. Beyond the wondrous wings, nearly every part of the bat body has evolved over time to meet the unique anatomical, physiological, and energetic requirements of being a flying mammal. These are especially pressing for female bats, who must fly while pregnant and carry their young pups as they forage.

The most obvious anatomical adaptation for flight in bats is the hand wing, which enables powered flight (see page 25). Composed of long, delicate bones across which a thin layer of living skin is stretched, this heavily modified mammalian feature is more than meets the eye. The skin of a bat wing (the patagium) is incredibly thin, delicate, and flexible, allowing it to stretch and move in ways that are essential for maneuverable flight.

The elasticity of the patagium allows bats to adjust the shape and curvature of their wings to support different speeds and flight maneuvers. Underlying this elasticity is an intricate network of blood vessels, muscles, and connective tissues. The rich supply of blood vessels maintains wing tissue integrity, facilitating the rapid healing of any injuries to the skin of the wing.

In some species, such as the Variegated Butterfly Bat (*Glauconycteris variegata*, page 84), the venation is part of the visible color patterns of the wings. The wing membrane is not simply a flap of skin but rather a living tissue that aids flight as well as gas exchange and thermoregulation. Since the blood vessels are so close to the surface, bats are able to bring in oxygen and expel carbon dioxide through the skin, increasing the efficiency of gas exchange during long, energetically expensive periods of flight. Through these wing blood vessels, they can also rapidly dissipate the body heat generated during flight and thus avoid heat stroke.

The long, delicate bones of the bat's fingers support the wing membrane. They are lightweight to save energy, but are under significant stress during powered flight. To compensate, bats have an extra bone at the elbow called the ulnar sesamoid. Formed when part of the triceps muscle ossifies, it functions to strengthen the joint. Similarly, for bats that have a wing membrane between the hind legs (a uropatagium), a spur of cartilage near the ankle, called the calcar, provides structural support for this unique bat structure. Interestingly, the skin of the uropatagium is thicker and more resilient than other parts of the wing membrane, which may help reduce damage from insect body parts when this structure is used as a scoop during prey capture. Although the bones of digits II through V of the hand wing are fully enclosed within the wing membrane, the thumb remains separate and typically has a claw, which may aid in climbing, roosting, and food handling.

↙↘ The Variegated Butterfly Bat is a well-known species from Sub-Saharan Africa. It is easily recognized for the reticulated patterning of its wings, formed by visible blood vessels and fibers of muscle and elastin. Like all other species in the family Vespertilionidae, it has a long tail that is fully enclosed in the uropatagium.

BATS IN FLIGHT AND AT REST

Myriad other skeletal, anatomical, and physiological modifications support the unique bat lifestyle. Bats in flight require approximately 12 times as much energy as bats at rest. To meet these needs they have a very efficient circulatory system, facilitated by oversized hearts and lungs housed within an enlarged rib cage and broad collarbones. Just as the human heart rate varies between exercise and rest, the bat heart rate during flight is significantly higher. In the well-studied Common Tent-making Bat (*Uroderma bilobatum*), the heart rate during flight can exceed 1,000 beats per minute, compared to around 200 beats per minute at rest. To support these exceptional cardiovascular needs, bat veins and arteries contract rhythmically to pump blood back to the heart. In other mammals, only the arteries do this.

To generate the power needed for flight, bats have exceptionally strong arm, back, and chest muscles. Similar to birds and pterosaurs, the chest muscles are supported by a keel on the sternum bone, providing more surface area for muscle attachment. Their enlarged chest, combined with a relatively small pelvis, gives them quite an exaggerated "body builder" appearance, especially compared to other mammals of similar size, such as rodents. In addition to the arm, back, and chest muscles, bats also have five muscles not found in other mammals, which control the tautness of the wing membranes and allow them to adjust the curvature of the airfoil during flight.

Bat bodies are not just modified for flight. There are also adaptations for extended periods of rest when bats are neither foraging nor migrating. The long, slender bones of the bat hind limb support these unique animals while they roost, hanging upside down. The arrangement of the tendons in the feet and the lower legs keeps their long and flexible toes firmly gripped on a branch or cave wall, with negligible energy required. This roosting position conserves energy and allows for rapid takeoff when needed.

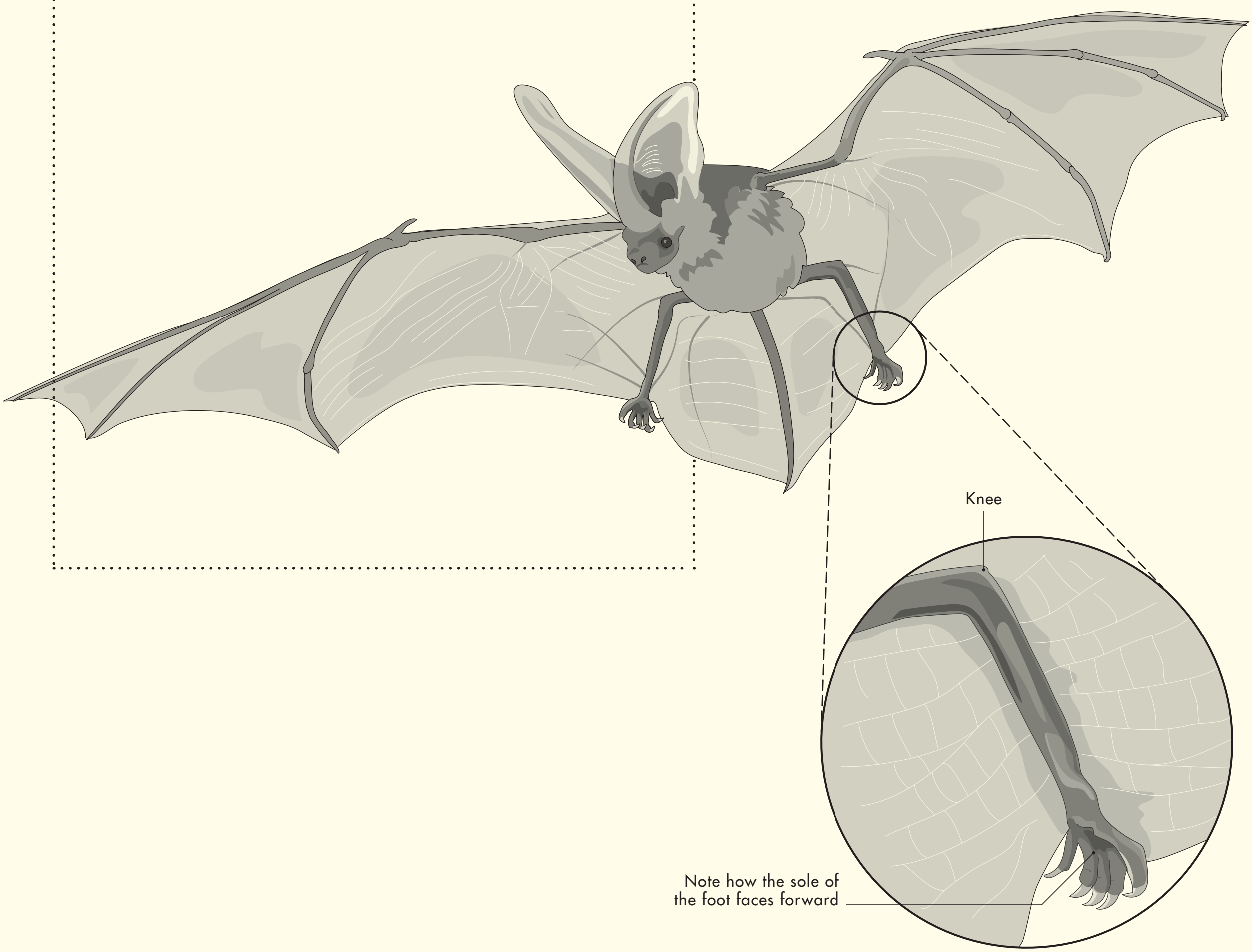
← Roosting bats, like this Common Sword-nosed Bat (*Lonchorhina aurita*), have resting heart rates significantly lower than bats in flight.

HIND LIMB POSITION

Perhaps the most surprising feature of the bat body is the rotation of the hind limbs at the pelvis, such that the sole of the foot faces forward. Accordingly, the bat knee flexes in the opposite direction compared to other terrestrial mammals. The position of the hind limbs contributes to the aerodynamic shape of the bat in flight, supports the uropatagium when present, and facilitates roosting, but it comes at a cost. Most bats, unlike birds, are not good at walking. Furthermore, although bats are highly skilled at taking off for flight, landing can be perilous. Some bats have four-point landings, touching down with hind feet and thumbs, while others land (somewhat awkwardly) on their feet. Amazingly, some bats do backward somersaults just before landing to direct their feet toward the substrate.

"Backward" leg

All bats have "backward" legs, rotated at the hip by 180°. Note the visible bending at the knee and the positioning of the foot such that the sole is visible when looking at a bat from the front. This shift in basic mammalian anatomy is often overlooked when we consider the many other amazing evolutionary changes present in bats.



← The New Zealand Lesser Short-tailed Bat (*Mystacina tuberculata*) is unusual in that it spends much of its time walking on the forest floor in chase of crawling rather than flying insects.

→ Spix's Disk-winged Bats are often found roosting in the small tube-like structures formed by the unfurled leaves of tropical plants.

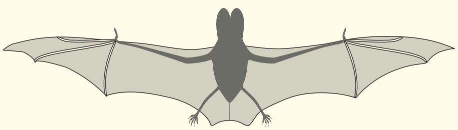
↓ Disk-like structures present on the wrists and ankles of Spix's Disk-winged Bats are a unique adaptation that helps them cling to the smooth and damp sides of these leaves.

VARYING APPEARANCE

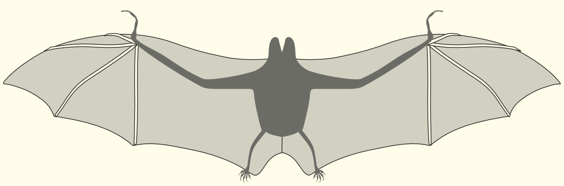
As we shall see throughout this book, because bats live in a remarkable variety of habitats and feed on many different food sources, they vary significantly in overall appearance and size. For example, wing shape varies according to lineage and niche, which is tied to flight differences. Likewise, the appearance of the bat head is strongly linked to both diet and echolocation patterns, with facial modifications for emitting echolocation calls and ear modifications for receiving their echoes. Some highly unusual bats have additional unique anatomical modifications, such as the sucker-footed bats of Madagascar (see the Eastern Sucker-footed Bat, *Myzopoda aurita*, page 82) and the disk-winged bats of South America, such as Spix's Disk-winged Bat (*Thyroptera tricolor*), which have skin at the wrists and ankles modified to form disk-like structures for clinging to smooth surfaces like unfurled leaves. Although the basics of the bat body are the same across all 1,482 species, the differences between bats reveal amazing evolutionary stories.

Wing shapes and flight

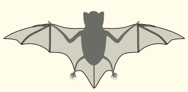
Every bat has "hand wings" and flies, but the size and shape of their wings vary significantly. Wing variation reflects differences in a bat's foraging ecology, including where it feeds, how it acquires its food, and what type of food it prefers.



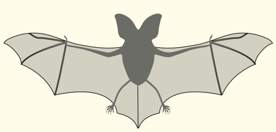
Large-eared Giant Mastiff Bat
(*Otomops martiensseni*)



Egyptian Rousette
(*Rousettus aegyptiacus*)



Moloney's Mimic Bat
(*Mimetillus moloneyi*)



Brown Long-eared Bat
(*Plecotus auritus*)

Wing shapes

Bats vary in overall body size and also in the shape of their wings. Some bats have short stubby wings while others have long narrow wings. Relative to their overall body size, bat wings can also be larger or smaller, as measured by their surface area.

Bat wings generally vary in two primary ways: size and shape. Wings can be smaller or larger relative to the overall size of the bat. This is measured by the surface area of the wing relative to the bat's weight, and is called "wing loading." Similarly, bat wings can vary in shape, ranging from short and broad to long and narrow. This is measured by the wingspan relative to the surface area of the wing and is called "aspect ratio." Bats within each of the 21 living bat families usually have similar wings, with notable exceptions tied to species differences in ecology.

Bats with a small wing surface area relative to their body size have high wing loading. They must work harder to generate the lift needed to stay airborne but are otherwise efficient fliers because the drag on their smaller wings in flight is less. Bats with high wing loading often also have long and narrow wings, with a high aspect ratio. These bats can fly very far and at very high speeds. They typically forage in open, uncluttered environments and catch their food on the wing. These modifications for speed and distance are advantageous when high speed and short migration time are needed, but they come at a cost, as these bats cannot turn tight circles and have less maneuverable flight in general. They are unable to forage in cluttered forests, nor to hover to gather food that does not move, like fruit and perched insects. They also have difficulty taking off and must roost in high-up locations so that they can drop down to build up airspeed before thrusting forward. Long, narrow wings are often found in long-distance migrating insectivorous bats like the free-tailed bats and the ultra-marathoner fruit bat, the African Straw-colored Fruit Bat (*Eidolon helvum*), as well as in fish-eating bats such as the Greater Bulldog Bat and the Fish-eating Myotis (*Myotis vivesi*)

↑ The Mauritian Tomb Bat (*Taphozous mauritanus*) has long, narrow wings (high aspect ratio) with a small surface area (high wing loading), which enables fast and energetically efficient flight.

→ The Indian Flying Fox can fly long distances, but also must be able to fly slowly and maneuver to land in trees. The compromise is wings that are quite long but have a large surface area.

that fly over open water with less need for tight turns. However, in this case they have wings with a relatively large surface area—that is, low wing loading—so that they can carry their heavy fish prey.

Bats with short and broad wings (low aspect ratio), like the Brown Long-eared Bat (*Plecotus auritus*), are the champions of flying and feeding in cluttered environments, even in the dense canopies of the tropical rainforest. They are agile fliers that are able to quickly adjust direction and speed. Although they are not typically long-distance or exceptionally fast fliers, they have extraordinary control during flight. Like other bats, they generate lift and thrust through the wingbeat cycle—the flapping of their wings. However, when needed, they can quickly fit through an opening barely larger than their body by tucking their wings in close to the body at just the right moment. Their ability to maneuver around obstacles is aided not just by their echolocation calls but also by small sensory hairs on the surface of their wings. These hairs allow the bat to sense changes in air pressure and speed over its wings and to adjust flight patterns accordingly. Bats with short and broad wings can either have wings with a relatively smaller surface area (high wing loading) or wings with a relatively greater surface area (low wing loading).

Species in the latter group are gleaners and hoverers, like the long-eared bats in the genus *Plecotus*. They select insect prey that is stationary, briefly hovering like a hummingbird, and have the wing

↖ The Lesser Long-nosed Bat (*Leptonycteris yerbabuenae*) is a nectarivore whose wing shape supports both hovering (short, broad wings) and fast flight (small surface area) between the patchily distributed flowers on which it feeds.

↑ The Brown Long-eared Bat has short, broad wings (low aspect ratio) with a large surface area (low wing loading), which allows them to hover and to carry off heavy prey items.

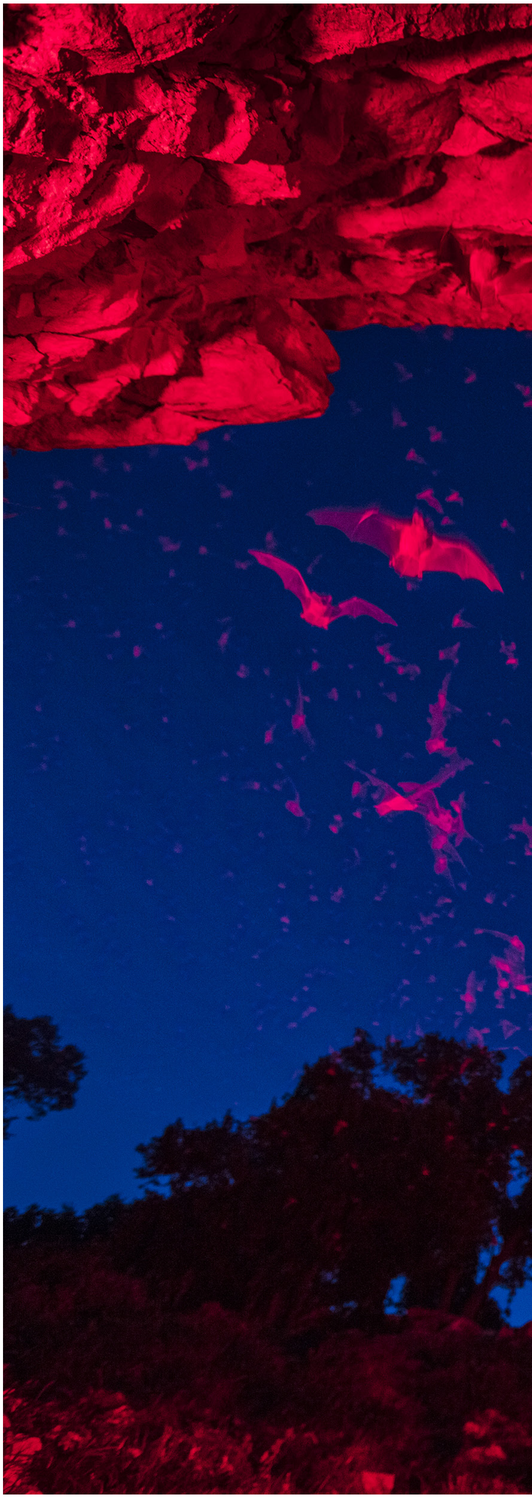
strength to carry off heavier food items. Gleaning bats will often carry their prey to a nearby perch where they can more easily manipulate them, leaving a pile of discarded insect body parts below.

Finally, bats may or may not have a well-developed uropatagium—a wing membrane between the hind limbs. This membrane, which may enclose the tail or part of it, can vary dramatically in shape. Potential roles for the uropatagium, beyond being used as a scoop for capturing prey, are not well understood, but it may aid in maneuvering during flight. Stretched between the hind limbs, it is functionally very different from a bird tail as its movements impact, and are impacted by, the rest of the bat wing.

How fast can bats fly?

Bats can reach speeds of up to 90 mph (144 km/h), but speed is highly species-specific. Some bats can hover like hummingbirds, extracting nectar from flowers, while others are able to achieve great flight speeds in search of faraway food sources.

The Brazilian Free-tailed Bat (*Tadarida brasiliensis*, page 274) is widely recognized as the fastest bat, at 90 mph (146 km/h), and one of the speediest flying animals in the world. This impressive speed is supported in part by high wing loading (small wing surface area relative to body size), long, narrow wings, enlarged pectoral muscles, and distinct air vortices created at the wingtip, which provide thrust. Free-tailed bats roost in exceptionally large numbers, ranging from hundreds to thousands to millions per site. At these high densities, bats emerge from their cave roosts as large columns of upwardly dispersing animals.



→ Brazilian Free-tailed Bats, shown here with thermal imagery, can congregate by the millions. They emerge nightly to feed from their roosts, which include caves and human-made structures like bridges.

As aerial pursuit predators of a variety of flying insects, each bat must separate itself sufficiently from its many roost mates in order to access food. Like pilots, bats can take advantage of the prevailing wind to increase their speed and to gain altitude for longer-distance travel.

Flight speed has only been measured in a few dozen other bat species, and not surprisingly varies by context. For example, Little Brown Myotis have been clocked at 5 mph (8 km/h) when flying over water (and potentially drinking), 11 mph (18 km/h) when hunting, and 18 mph (29 km/h) when approaching cave roosts (and not foraging).

For bats that roost and forage within cluttered forest environments, maneuverability rather than speed is the more important metric. At the lowest end of the bat speed continuum, hovering in place represents its own flight challenges but is energetically less costly than directional flight. Newer techniques that deploy

↖ Prior to nightly emergence, Brazilian Free-tailed Bats warm up by flying inside their cave roost for some time.

↑ To get a head start and distance themselves from their neighbors, some Brazilian Free-tailed Bats emerge from their day roosts before dusk to travel in search of food.

high-speed videography and the use of strategically placed sensors to analyze 3D kinematics are advancing our understanding of bat speed and other aspects of flight. Likewise, the increasing miniaturization of GPS tags allows for the georeferenced tracking of bat movements, including speed, across the landscape.

How far can bats fly?

Bat flight distances vary across species. Some bats find their nightly meal close to home while others can travel 60 miles (100 km) or more each night in search of food. Likewise, some bat species remain localized all year round, while others migrate great distances.

Nightly foraging patterns, including how far bats fly each night and which routes they take, are typically studied using radiotelemetry or GPS tracking. Not surprisingly, the fastest bats, with their specialized wings, forage the farthest and can migrate long distances. For the Brazilian Free-tailed Bat, individuals may fly 30–60 miles (50–100 km) per night and may reach altitudes of over 10,000 ft (3,000 m), where prey is abundant. While migrating, they might travel 220 miles (350 km) in a night, eventually covering 1,050 miles (1,700 km) from the southern United States to Mexico.

← Lightweight radiofrequency tags can be used to track bat flight patterns and distances. Pallas's Long-tongued Bat is a nectar feeder that follows the same route each night. The symmetrical holes in this bat's wings are from tissue biopsies taken to obtain a DNA sample. Bats have no issues flying with small holes or tears in their wings, which heal within two to three weeks.

↗ Bechstein's Myotis from Europe and Western Asia is a forest-dwelling species. Maternity colonies form each spring.

In contrast, the smallest bat in the world, the Hog-nosed Bat from Thailand and Myanmar, is believed to only forage within about half a mile (1 km) of its limestone cave roosts and may disperse no more than 1–3 miles (2–5 km) across its entire life span. The biggest bats, flying foxes such as the Large Flying Fox, are highly mobile and within a year can travel hundreds of miles between roosting sites, readily hopping between Southeast Asian island nations. Similarly, within Africa, the Straw-colored Fruit Bat smashes records with its cross-continental annual migration between Central Africa and Zambia—a distance of more than 1,500 miles (2,500 km).

Some bats readily explore new areas, but many are creatures of habit. In common with hummingbirds, nectar-feeding bats, such as Pallas's Long-tongued Bat (*Glossophaga soricina*), often display a nightly travel pattern called "traplining," in which they repeat the order in which they visit specific locations. Bat flight patterns and distances traveled often also vary by sex, with females of some species more likely to migrate than male bats. In addition to nightly flight patterns and migrations, which occur in regular daily or annual cycles, some bats undertake a once-in-a-lifetime dispersal when they are young, moving away from their natal group. For example, in the temperate bat species Bechstein's Myotis (*Myotis bechsteinii*), females typically remain near where they were born and often reside with their original birth colony, while males disperse to new geographic regions.

↑ The migratory Nathusius's Pipistrelle is widely distributed across Europe, typically following a northeastern-southwestern route.

MIGRATION FUEL

Although nightly foraging is generally fueled by food acquired each night, for those species that migrate, prolonged long-distance flight is mostly fueled by stored fat. Many species prepare for this marathon by weeks-long bouts of excessive eating and fat deposition. This is especially true for temperate bats like the 0.3 oz (8 g) Nathusius's Pipistrelle (*Pipistrellus nathusii*), which holds the record for small bat migration—with a journey of over 1,380 miles (2,224 km) from Latvia to Spain. The secrets of some migratory species, such as Nathusius's Pipistrelle, have been revealed by the ringing of bats, tracked over time by a host of international bat biologists.

Record holder

Nathusius's Pipistrelle holds the record of migration by a small bat species. A male banded or ringed in Pape Nature Park in southern Latvia in 2015 was recovered in Pitillas' Lagoon Nature Reserve in Northern Spain in March 2017.

Bat coloration

Most bat species have fur that ranges from gray to brown to rust-colored. Some bats have darker fur on their backs compared to their abdomens. Striking facial and body patterns of stripes, neck collars, and spots are also found in bats throughout the world, especially those that roost in vegetation.

Mammals like bats are less colorful than other animals, particularly when compared to the other flying vertebrates, the birds. Indeed, with their range of vivid colors and patterns, and males that are typically much more vibrant than females, birds utilize the full visual spectrum. As nocturnal animals that roost during the day, and thus need to hide from predators while roosting, most bat coloration patterns serve to conceal them, enabling them to resemble or match the natural background of their environment.

Concealment can be achieved in a variety of ways, including crypsis (or camouflage), in which overall body color resembles that of the habitat; pattern blending, in which body color patterns match patterns of light and

dark in the environment; and disruptive coloration, in which irregular marks or contrasting colors break up the body's recognizable contours.

The most common pelage (total body fur covering) pattern in bats is uniform—all one color—often a shade of gray, brown, or rust-colored fur. For bats, especially those that roost in large numbers in caves or tree hollows where little concealment is required, this basic coloration is likely all that is needed. When a color pattern is present, the most common form is countershading, in which the fur on the back is darker than that on the abdomen. The fur color gradient creates an optical illusion, making the animal less noticeable when viewed by avian predators from either above or below.

← Decken's Horseshoe Bat (*Rhinolophus deckenii*) displays the most common fur color of bats, brown, with the belly fur sometimes lighter than the fur on the back.

↑ Welwitsch's Myotis (*Myotis welwitschii*) has highly patterned wings, with the typical dark bat wing membrane interrupted by reddish skin regions that follow the wing bones.

STRIPES, NECK COLLARS, AND SPOTS

The next most prevalent bat pelage patterns are stripes, neck collars or bands, and spots (in that order). Stripes serve to visually subdivide an animal's overall shape into separate components, making a predator's perception of the whole animal more difficult. Some bats with stripes, especially on their faces, are tent makers, including the Common Tent-making Bat (*Uroderma bilobatum*).

Tent-making bats modify leaves, stems, and other plant parts to make a shelter from which they roost upside down. When viewed from below, their facial stripes serve to disrupt their overall appearance. The all white fur of the most well-known tent-making bat, the Honduran White Bat (*Ectophylla alba*, page 78), may similarly help them avoid predation, as lightly colored objects are hard to discern against a sunlit background. This species, and many of the other tent makers, often exhibits yellowing of the skin (ears, nose leaves, arms and legs) due to consumption of carotenoids. This yellowing mirrors the primary color reflected on the underside of the *Heliconia* leaves used for their tents—suggesting that the yellow markings serve to disrupt the overall visual form of these clustered bats and help conceal them within their highly specialized roosts.

The yellow facial skin of Honduran White Bats may have one additional role: communication. Fur and skin colors and patterns are used in social interactions in other mammals. Whether bat markings contribute to communication is poorly understood despite the fact that we know bats have good vision and many can see color. The Honduran White Bat displays sexual dichromatism—different coloration in males and females. In adulthood, the yellow color of the nose leaf becomes brighter, especially in males in better body condition. This strongly suggests that it signals a male's quality to potential mates in a manner reminiscent of many bird species, where healthier males are brighter.

Finally, the presence of neck bands or differently colored "collars" in some bats are also believed to play a role in concealment, as are the less frequent spots seen in some bat species. The Spotted Bat (*Euderma maculatum*, page 80) is perhaps the most iconic of bats with spots, but the reason for its striking pelage (and its nearly clear wings) is unknown. Bright yellow spots along the wing membranes, ears, and nostrils are common among the Tube-nosed bats and likely serve as camouflage through disruptive coloration. Unusual wing patterns, including visible variegation and translucent wings, are also found in bats of the African genus *Glauconycteris*, which include the Variegated Butterfly Bat (*G. variegata*). This clade of bats also includes the Badger Bat (*G. superba*) with its "superb" stripes, neck band, and spots. Much remains to be learned about the reasons for bat coloration.

← The wavering stripes down the back of the Greater Sac-winged Bat (*Saccopteryx bilineata*) disrupt its appearance and provide camouflage.

→ The Common Tent-making Bat has stripes on its face, which provides disruptive camouflage and makes it less recognizable as prey.

EIDOLON HELVUM

African Straw-colored Fruit Bat

Gregarious, long-distance migrator

SCIENTIFIC NAME	*Eidolon helvum*
FAMILY	Pteropodidae
DIET	Fruit, flowers, and leaves
HABITAT	Lowland forests and savanna zones
CONSERVATION STATUS	Near Threatened
WEIGHT	8.1–12.3 oz (230–350 g)
WINGSPAN	29–37 in (72–95 cm)

African Straw-colored Fruit Bats are one of the largest and the most visible species in Africa. This vocal and highly social tree-roosting species congregates in the thousands, often in close vicinity to people.

This species is broadly distributed across African savanna zones and lowland rainforest and extends into the southwestern Arabian Peninsula. Highly adaptable, African Straw-colored Fruit Bats can also be found in coastal and riverine forests and are often recorded in urban settings, such as wooded city parks. As highly visible and large bats, often considered a nuisance, they are heavily harvested by locals for meat in West and Central Africa. A preferred food item in both rural areas and cities, bats are sold live or freshly killed, potentially spreading viruses and other pathogens to humans. Locating colonies is made easier by the nearly constant squawks, shrieks, and barks they emit. Hunting, along with habitat loss through removal of roost trees, is a major contributor to ongoing population declines.

Some colonies have been estimated to have over 1 million bats, which break up into smaller groups of about 100 for sleeping. These numbers peak in February through May of each year, when females give birth to their one yearly pup. Although some African Straw-colored Fruit Bats are non-migratory, millions will fly over a thousand miles during their annual migration. For a few weeks each year, upward of 8 million bats converge at Kasanka National Park in Zambia to feed in the seasonal swamp forests. Scientists have used GPS dataloggers to study this ecologically important seed-disperser—documenting nightly foraging distances of nearly 62 miles (100 km). This species is easily recognized by its bright yellow, orange, or brown shaggy collar around its throat and neck and by the straw-colored fur on its head and back.

→ African Straw-colored Fruit Bats are highly social and roost in trees in close proximity to each other.

ECTOPHYLLA ALBA

Honduran White Bat

Tropical tent maker

SCIENTIFIC NAME	*Ectophylla alba*
FAMILY	Phyllostomidae
DIET	*Ficus colubrinae* fruits
HABITAT	Subtropical/tropical, moist lowland forest
CONSERVATION STATUS	Near Threatened
WEIGHT	0.16–0.25 oz (4.5–7 g)
WINGSPAN	8.7–9 in (222–231 cm)

The Honduran White Bat is easy to identify with its white fur and yellow skin. It chews large *Heliconia* plant leaves along either side of the midrib, causing the sides to fall down and create a tent for roosting.

This small bat species is found in Caribbean lowlands from Honduras to western Panama, inhabiting forests up to 2,300 ft (700 m) above sea level. As a tent-making specialist, Honduran White Bats need forests with high canopy cover and low understory cover, so they can find the newly opened leaves out of which they make their roosts. Groups of four to eight individuals create tents in leaves 3–6 ft (1–2 m) above ground. The group's single male and multiple females roost together until pups are born, after which the male may leave. Lactating females leave their pups to find fruit and may return to the tent to nurse the pups up to six times per night.

The Honduran White Bat is in the family Phyllostomidae, which have "nose leaf" protuberances on their faces that aid the emittance of echolocation calls. Their bright yellow skin, caused by ingested carotenoid pigments, is most visible in the nose leaf and ears. Combined with their white fur, it has been suggested that the yellow skin might help them blend in with the daytime yellowish-green dappled light that passes through the leaves of their roosts. As is often the case in wildlife species with very specific habitat needs, the Honduran White Bat is especially susceptible to the effects of habitat loss and is currently in significant decline.

→ Honduran White Bats are one of several species of bats with white or nearly white fur. Their yellow skin may signal health status to other bats, and is brighter in males.

EUDERMA MACULATUM

Spotted Bat

Solitary and beautiful

SCIENTIFIC NAME	*Euderma maculatum*
FAMILY	Vespertilionidae
DIET	Large moths and occasionally beetles
HABITAT	Varied, including arid regions, ponderosa pine forests, and marshlands
CONSERVATION STATUS	Least Concern
WEIGHT	0.57– 0.71 oz (16–20 g)
WINGSPAN	Around 14 in (35 cm)

The Spotted Bat's large, white spots stand out against the shaggy, black fur on its back and are accented by large, nearly translucent ears and wings. Considered rare, the Spotted Bat forages alone for large moths and the occasional beetle.

The Spotted Bat's pelage is unique among the bats in the family Vespertilionidae. Among these vesper bats, the largest of the bat families, only those in the Old World genus *Glauconycteris* have comparable striking fur patterns. Female Spotted Bats time the birth of their single pup for the summer months, when food availability is greater. Pups are born without spots and with ears not yet fully developed. Outside of mother–pup relationships, individuals are dispersed and rarely interact. Separated by distances of 2,500–3,300 ft (750–1,000 m), they may use vocalizations to communicate with neighbors.

Distributed patchily across western North America, from British Columbia in southwestern Canada and Montana and Wyoming in the United States to Querétaro in central Mexico, the Spotted Bat is an example of a species that is naturally rare. This may be tied to its use of rocky cliffs with snug cracks for day roosts, which are limited in availability. Although this habitat is required for roosting, large, open foraging sites are likely important for hunting. Indeed, this species has been documented in many different habitat types, including desert shrub and arid areas, wetlands and open areas near water, riparian habitats, woodlands, and old agricultural fields. It has been captured below sea level in California and at elevations up to 9,800 ft (3,000 m) in Mexico.

→ Easily recognized by their unique appearance, Spotted Bats prefer to roost in the crevices of vertical cliff faces.

MYZOPODA AURITA

Eastern Sucker-footed Bat

Clings to smooth surfaces

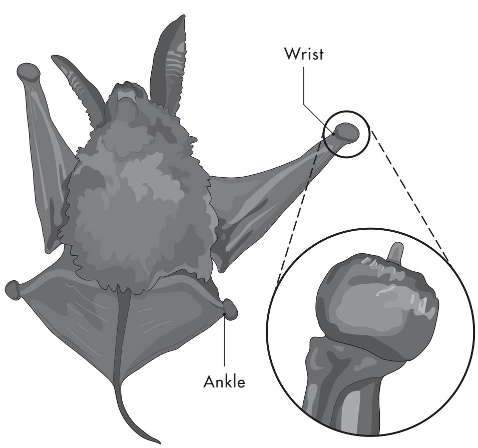
SCIENTIFIC NAME	*Myzopoda aurita*
FAMILY	Myzopodidae
DIET	Moths, beetles, and other insects
HABITAT	Lowland and littoral forests, disturbed areas
CONSERVATION STATUS	Least Concern
WEIGHT	0.32–0.34 oz (9–9.5 g)
WINGSPAN	Not known

The Eastern Sucker-footed Bat has distinctive, round, sucker-like structures on its wrists and ankles. Using wet adhesion, these allow the bat to climb up and adhere to the smooth surfaces of traveler's palm leaves. It has long, wide ears, with a mushroom-shaped basal structure not found in any other bat lineage.

The Eastern Sucker-footed Bat is one of two species in the family Myzopodidae, which is endemic to the island of Madagascar. This unusual bat lineage's placement within the bat family tree is not fully resolved, even with modern molecular techniques used to study the relationships between organisms. Several lines of evidence, including morphological and molecular similarities, suggest they are closest to the group of bats that includes the sheath-tailed bats in the family Emballonuridae and the slit-faced bats in the family Nycteridae. Fossils from species allocated to the Myzopodidae have been uncovered in Egypt, suggesting an ancient and African origin for this unusual group of bats.

Sucker-like structures in the Eastern Sucker-footed Bat display convergent (or parallel) evolution with the sucker-cups on a different species, the Spix's Disk-winged Bat, meaning that the presence of an adhesive structure evolved separately in each group of bats but arose because it serves the same purpose.

The Eastern Sucker-footed Bat is found in the humid zone of eastern and northeastern Madagascar and primarily eats moths and beetles. Unlike many bat species, Eastern Sucker-footed Bats are able to survive in highly modified habitats, which has allowed them to persist despite the significant deforestation that has occurred in Madagascar.



Wrist pad

Unlike Spix's Disk-winged Bat, the Eastern Sucker-footed Bat uses wet adhesion to cling to surfaces; its wrist and foot pads are not concave and do not enable true suction.

→ The Eastern Sucker-footed Bat is one of a few bat species that roosts head up, prepared to meet an animal that may enter its tiny roost.

GLAUCONYCTERIS VARIEGATA

Variegated Butterfly Bat

Beautiful variegated wings

SCIENTIFIC NAME	*Glauconycteris variegata*
FAMILY	Vespertilionidae
DIET	Soft-bodied insects
HABITAT	Open savanna
CONSERVATION STATUS	Least Concern
WEIGHT	0.18–0.5 oz (5–14 g)
WINGSPAN	Around 12 in (30 cm)

The Variegated Butterfly Bat is the most striking of the bats within the colorful and patterned genus *Glauconycteris*. It is widely but patchily distributed throughout much of sub-Saharan Africa.

The soft, dense fur of the Butterfly Bat is multicolored on the back, with pale cream to pale yellow at the base and darker yellow verging on orange at the tips. The fur on the belly is much lighter. Butterfly Bats have relatively small, rounded ears for bats in this family and a muzzle that appears swollen due to glandular protuberances that separate the nostrils. Their wings and the uropatagium are pale yellowish-orange with dark brown pigment outlining their bones and the veins that traverse the wings, and are thus described as reticulated. Females are slightly larger than males.

A related bat, Machado's Butterfly Bat (*Glauconycteris machadoi*), known only from a single Angolan specimen with dark pelage, is believed by some scientists to be a melanistic form or mutant of the Variegated Butterfly Bat due to its similar morphology and reticulated wings. Genetic analysis to resolve whether this is simply a color variant of the Variegated Butterfly Bat or a distinct species is needed.

Variegated Butterfly Bats generally roost in dense clusters of leaves in small groups of 3 to 12 individuals. Perfectly camouflaged by their reticulated wings, which resemble dead leaves when the bat is roosting, this species is nearly impossible to see in the roost unless they move. Unlike many bats, the Variegated Butterfly Bat can take off from the ground. Despite being so much easier to identify than many other bat species, much remains unknown about its basic biology and ecology.

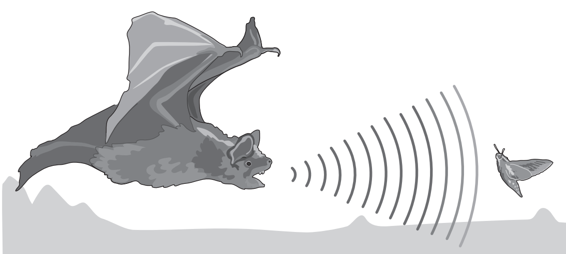
→ Sometimes called the Leaf-winged Bat, two subspecies of the Variegated Butterfly Bat are recognized; one in the northern part of its range and one in the southern part of its range.

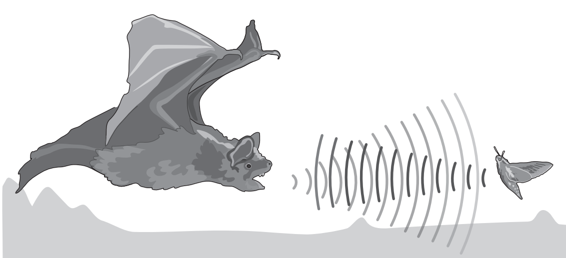
ECHOLOCATION

Echolocation origins

Echolocation is the extraordinary ability to translate returning sound wave echoes into mental pictures. It allows animals to "see" with sound. The use of biological sonar is not unique to bats, but in them it has reached a state of evolutionary perfection.

At its most basic, echolocation consists of emitting a sound and using the returning echoes of that sound to navigate. Echolocation has evolved independently in a number of animal groups, including the toothed whales, dolphins and porpoises, shrews and tenrecs, bats, a handful of birds, and the occasional human. In bats these sounds can be produced in the larynx or "voice box" (most bats), by clapping the wings (several species), or by clicking the tongue (up to eight species).





The echolocation calls of some species can be faintly detected by humans. However, the vast majority of bat species produce sounds above the range of human hearing (ultrasonic). This explains the mystery described in the late 1700s by Italian scientist Lazzaro Spallanzani and the Swiss physician Louis Jurine, who demonstrated that blind bats could navigate perfectly well but failed when their ears were plugged. Without being able to detect bats' ultrasonic signals they were at a loss to explain this "ear navigation." It wasn't until the 1930s that the mystery was solved, when American scientist Donald Griffin deployed a newly developed apparatus capable of detecting sounds above the human hearing frequency range. In the approximately 100 years since the discovery of the ultrasonic world of bats, the sophistication and diversity of bat echolocation signals and neural processing capabilities has been heavily studied—and has even informed the development of sonar and radar technology.

Returning echoes

Many bats use echolocation to navigate and to detect prey by emitting calls and listening to returning echoes, which bounce off prey and other objects.

Echolocation likely evolved in tandem with flight in bats, but physiological and behavioral traits such as sound production and hearing are not easily interpreted from the fossil record—especially since the skulls of the oldest bat fossils have been crushed by the fossilization process. This problem was recently resolved when a three-dimensionally preserved, 50-million-year-old skull was unearthed in France. After examining the shape of the cochlea in the inner ear and other regions of the skull, researchers concluded that it appears to have been capable of advanced laryngeal (from the larynx) echolocation, suggesting that advanced echolocation likely evolved only once in bats, a very long time ago.

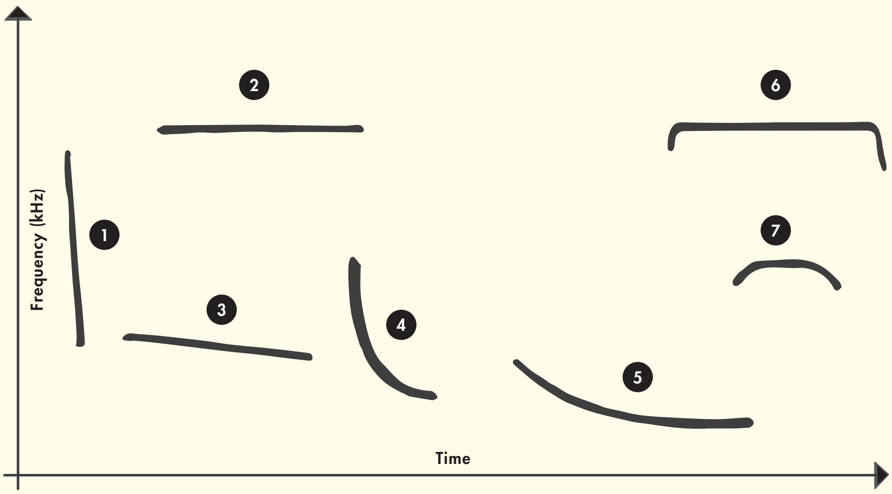
↑ The Common Pipistrelle (*Pipistrellus pipistrellus*) is a frequently captured species in Europe and may have been the species in which Spallanzani discovered the bats' ability to see with sound.

Echolocation basics

Ultrasonic echolocation calls are generated as vibrations and beamed out into the world through the bat's mouth or nose, or sometimes both. These sound waves bounce off objects to generate an echo, which is then interpreted by the bat's sophisticated auditory and neural pathways.

Sounds originate in the larynx, a hollow tube that lets air pass from the throat to the windpipe. Muscles in the larynx control its opening and closing and change the shape and tension of its walls. As air passes through the larynx, the phonatory muscles vibrate to produce sound, which then ripples away in the form of sound waves. The rate at which a vibration occurs is its frequency, measured in hertz (Hz), or the number of sound waves per second, and frequency is inversely related to wavelength. The longer a wavelength (measured in millimeters), the fewer wavelengths can occur per second. Low-frequency sounds are low-pitched, while high-frequency sounds are high-pitched. The lowest frequency bat sounds, such as those produced by the Spotted Bat, fall within the upper range of human hearing (20–20,000 Hz) and can be perceived by us.

→ The Spotted Bats' audible low-frequency echolocation calls travel farther than the higher calls typical of most bats and allow them to successfully forage in open areas.



Visualizing echolocation calls

Bat echolocation calls can be recorded using specialized "bat detectors" that record frequency, intensity, and time, as visualized on figures called sonograms.

1. Whiskered Myotis (*Myotis mystacinus*)
2. Mediterranean Horseshoe Bat (*Rhinolophus euryale*)
3. Southern Yellow Bat (*Lasiurus ega*)
4. Common Serotine Bat (*Cnephaeus serotinus*)
5. New Zealand Lesser Short-tailed Bat (*Mystacina tuberculata*)
6. Greater Horseshoe Bat (*Rhinolophus ferrumequinum*)
7. Lesser Sac-winged Bat (*Saccopteryx leptura*)

Echolocation calls of most bat species range between 20,000 and 120,000 Hz (20–120 kHz). Why do bats use such high frequencies for echolocation? On the practical side, few other sounds in nature exist in this range, which reduces potential interference. As echolocation is largely a short-range navigation system, the ability to send and then respond to the echoes of a high-frequency signal, which dissipates rapidly with distance, allows for navigational precision. Furthermore, different bat species utilize different frequencies, which may keep bats of one species from interfering with the echolocation of other species.

Most important, however, is the impact of high-frequency sounds on target discrimination—specifically the ability of a bat to detect small insects. Remember that high-frequency sounds have the shortest wavelengths and consider that the best wavelength for detecting an object is one that matches the length of the object. Calls consisting of wavelengths longer than an object's size will wrap around the object and thus distort the returning echo, whereas calls that match an object in size echo back more precisely. Calls at 30 kHz have wavelengths of 11.5 mm—perfect for localizing moths with high precision.

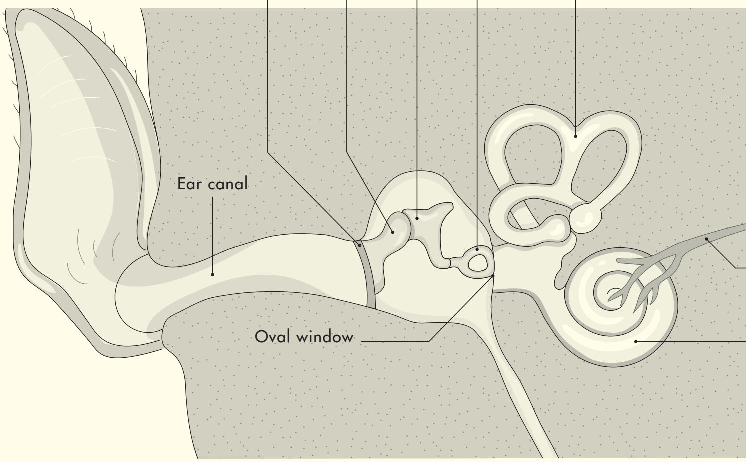
AMPLITUDE AND FREQUENCY

Another important attribute of sound waves is their amplitude, or the amount of energy put into the sound, which is measured in decibels (dB) and describes loudness. With some interesting exceptions, most bat calls are very loud—which ensures that an echo of sufficient strength is returned. We can be thankful that bat echolocation calls are ultrasonic (above our hearing range), as they would otherwise be painfully loud! Some "gleaning" bat species, whose food sources do not move, emit low intensity, or "whispering," echolocation calls. The Cuban Flower Bat (*Phyllonycteris poeyi*, page 112) is one example. An important pollinator on the Caribbean islands of Cuba and Hispaniola, this bat feeds from large, open-structured flowers. Recent studies, however, have demonstrated that multiple species of supposed whispering bats are louder than previously believed and can vary their calls by context (for example, by emitting louder calls in open areas where sound must travel farther).

Echolocation calls are nearly always a combination of sounds of more than one wavelength (and hence frequency) and more than one amplitude (intensity or loudness). Furthermore, bats do not emit echolocation calls continuously but rather in discrete pulses. Calls are typically characterized as either frequency modulated (FM) or constant frequency (CF) but, in reality, few bats use pure CF calls and many use a combination of CF and FM sounds. More useful descriptors are "narrowband" for calls that are mostly CF (span less than 10 kHz) and "broadband" for FM calls, which typically encompass a large range of frequencies. Bats may detect prey with narrowband CF or shallow broadband FM signals, but nearly all will switch to steep broadband signals at close range.

← Surveys of bat activity often involve the recording of bat echolocation calls over time by bat detector devices stationed near known bat areas such as cave entrances.

↗ The echolocation calls of the Painted Woolly Bat (*Kerivoula picta*) are characterized by broadband calls that start at relatively high frequencies of about 160 kHz and rapidly drop to around 40 kHz.



Anatomy of the bat ear

Sound waves that reach the eardrum, or tympanic membrane, are transferred to the inner ear and transduced into electrical impulses that travel along the auditory nerve to the brain.

MAKING AND HEARING SOUND

Most bat species emit sounds from their mouth, and thus fly with their mouths open. Bats from a handful of families project ultrasonic echolocation calls through their noses (and fly with their mouths closed). Within the pteropodid fruit bats of the Old World, who have evolutionarily lost laryngeal echolocation, two alternative mechanisms for generating sounds for echolocating have evolved in cave-roosting species. Several species, including the Lesser Dawn Bat (*Eonycteris spelaea*), produce clicking sounds by clapping their wings. The Egyptian Rousette (*Rousettus aegyptiacus*, page 242) has (re)developed the ability to see through hearing by producing clicks with its tongue. The six other *Rousettus* species and the Long-haired Rousette (*Stenonycteris lanosa*) also produce tongue clicks but their echolocation function has not yet been demonstrated in all of these bats.

Perceiving and interpreting echoes requires excellent hearing and so bats generally have large external ears, or pinnae. Echolocating bat ears also typically have a tragus, a cartilaginous projection from the base of the ear. The shape of this ear–tragus combination is designed to receive calls within 40 degrees of either side of the midline, focusing the sensitivity of the bat to incoming echoes. Bats can move their heads up and down and from side to side to scan for incoming echoes and also control the shape of their ears through minute muscles to fine-tune the information received by each ear.

Sound waves entering the ear vibrate the tympanic membrane, or eardrum. These vibrations are then passed along the three inner ear bones (malleus, incus, and stapes) to the oval window. From the oval window, vibrations are then passed to the spiral canal of the cochlea in the inner ear. Within the cochlea, tiny sensory cells, each specific to a particular frequency, are triggered and pass electrical impulses to the brain via the auditory nerve. The brain interprets these nerve impulses and acts upon the information with extraordinary speed, triggering changes in flight path, call production, and hunting strategy.

ECHOLOCATION CHALLENGES

The efficiency and precision of the echolocation system is extraordinary, but also presents some challenges to the bat. Since high-frequency calls dissipate rapidly from their point source and echo back softly, most bat calls are very loud when emitted so as to be sufficiently audible upon return. Thus, bats risk deafening themselves by virtue of the very loud sounds they produce. One solution, adopted by the Big Brown Bat (left) (*Eptesicus fuscus*, page 110) and others, is to temporarily deafen themselves during call emission, reserving their best hearing sensitivity for the period between calls. To do this, they utilize one of the tiny muscles in the ear, the stapedius, to pull the stapes away from the oval window during active call emission. At the end of the call this muscle relaxes, restoring hearing—an ingenious solution.

↑ The Lesser Dawn Bat uses a rudimentary system to echolocate in caves. It produces clicking sounds by clapping its wings and then interpreting the returning echo.

Integrating call and echo

Generating and responding to complex echolocation calls and their variable returning echoes occurs in milliseconds. Bats can turn their heads and ears to adjust sound production and reception and may rapidly change call patterns, especially when they are hunting.

Echolocation is often depicted as a bat emitting a series of discrete sound waves aimed in a single direction, from which echoes return. In reality, bats can change the width and direction of their acoustic beam by aiming their heads toward a target and by changing the shape of their mouth or, for some bats, their nose leaf. Similarly, bats can move their heads and even their ears to improve their ability to hear.

Bats use echolocation both for navigation and for finding food, and calls may differ depending upon bat species and the environment. However, when hunting, especially for flying insects, the observed echolocation patterns are similar across many bats and include a search, approach, and terminal phase. Each phase has a distinct call pattern in which call duration, bandwidth, and pulse rate vary.

In the search or hunting phase, most bats emit short-duration broadband pulses (2–5 milliseconds) followed by a pause to listen for returning echoes; this strategy is called "low duty-cycle echolocation." As all sound travels through air at the same speed of 340 meters per second, bats can interpret the time difference between the call and echo to calculate how far away the insect is. For example, the echo from an insect 3 ft (1 m) away returns 5.9 milliseconds after the emitted pulse. Short-duration calls ensure that the echo is not received prior to the call being completed.

Once an insect has been detected, the bat enters the approach phase, where frequency modulation (FM) may be steeper and pulses shorter.

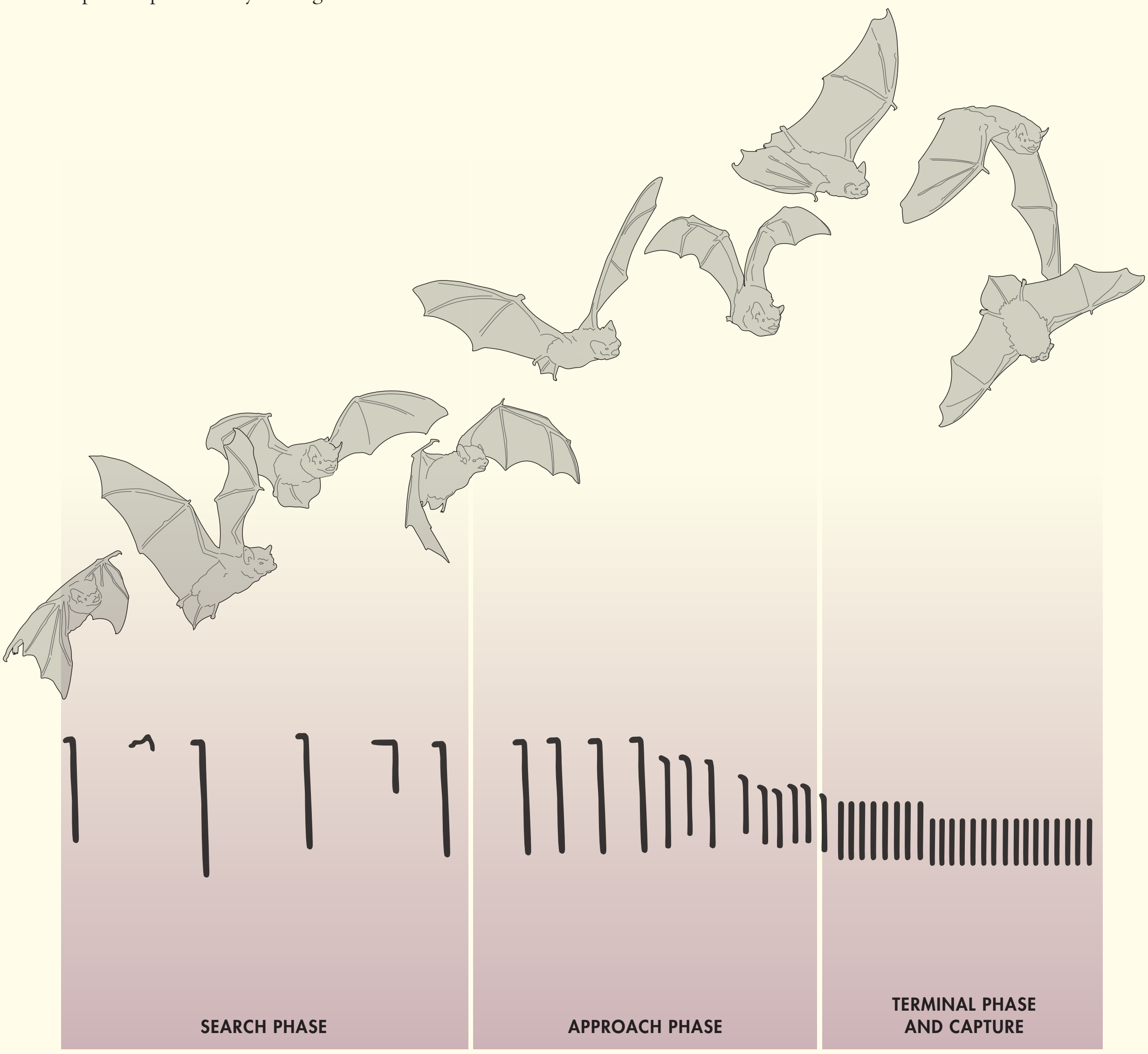
← Bats, such as this Greater Horseshoe Bat, emit echolocation calls more frequently as they get closer to their insect prey.

Shorter pulses decrease the overlap between call and echo. As the bat gains more rapid information on the insect's location, its calls get shorter and more frequent.

Finally, in the terminal phase, a bat fine-tunes its capture strategy with even more frequent short-duration calls, which results in capture. Even bats that use constant frequency or narrowband calls when searching will add a frequency modulated tail to their calls and may switch to broadband as they get closer to their prey due to the more detailed three-dimensional mental picture provided by FM signals.

Echolocation of the hunt

Bats change the nature of their echolocation calls during the search, approach, and terminal phases and capture of a feeding bout, which lasts mere seconds. A brief period of silence occurs as the bat chews its prey and the cycle repeats.



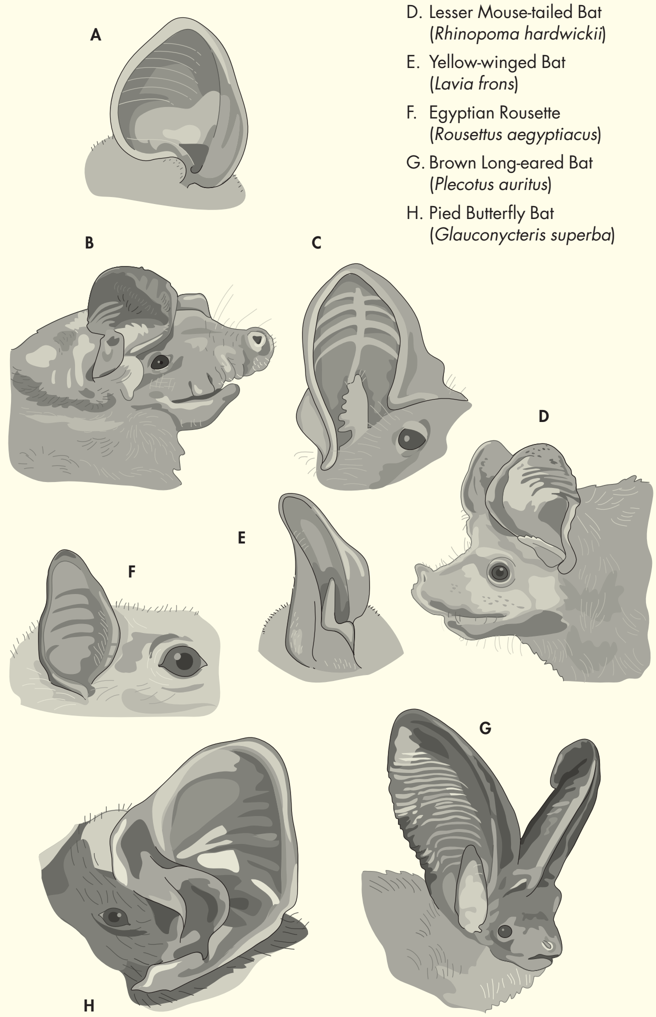
Nose leaves, loose lips, and big ears

The beautiful and sometimes bizarre diversity of bat faces and ears is extraordinary. This variety is intricately tied to echolocation and, in some cases, diet, which are both key to the remarkable evolutionary success of bats. Modifications for emitting sound depend on whether bats emit signals from their mouth or nose. Modifications to the ear optimize the perception of call echoes.

Ear shapes

Myriad ear shapes have evolved across the 21 families of bats to support the efficient detection of echolocation calls.

A. Bicolored Leaf-nosed Bat (*Hipposideros bicolor*)
B. Angolan Free-tailed Bat (*Mops condylurus*)
C. Common Vampire Bat (*Desmodus rotundus*)
D. Lesser Mouse-tailed Bat (*Rhinopoma hardwickii*)
E. Yellow-winged Bat (*Lavia frons*)
F. Egyptian Rousette (*Rousettus aegyptiacus*)
G. Brown Long-eared Bat (*Plecotus auritus*)
H. Pied Butterfly Bat (*Glauconycteris superba*)



The ancestor to all known living bats almost certainly emitted sound through the mouth, in a similar way to how social vocalizations are emitted. The majority of bats today still utilize this strategy and are called "oral emitters." That they are echolocating is evidenced by their open mouths during flight, as they aim echolocation pulses toward potential targets. Some bats, like mustached bats in the genus *Pteronotus*, form a tunnel of sorts with their fleshy lips, focusing their emitted signals.

An alternative strategy of emitting echolocation calls from the nose rather than the mouth has evolved independently in multiple bat lineages, and at least a few bat species, including the Brown Long-eared Bat, use both strategies. Deemed "nasal emitters," bats using this strategy have the advantage of being able to chew and call at the same time, which may be especially important for efficiently processing larger prey like moths. The majority of nasal emitters project sound through a specialized "megaphone-shaped," fleshy nose-leaf structure surrounding the nose, such as that found in the Australian False Vampire Bat (*Macroderma gigas*). Changes in nose-leaf shape due to underlying muscular control can affect the structure of outgoing calls and may be reflected in the acoustic views created by returning echoes. Over half of the roughly 455 bat species with nose leaves are in the megadiverse family Phyllostomidae (New World nose-leaf bats), followed by the Old World bat families Rhinolophidae (horseshoe bats) and Hipposideridae (Old World nose-leaf bats).

Bat ears are often large compared to those of other mammals because the hearing of bats is critical to their survival and evolutionary success. Both the overall size and shape of their ears vary significantly across species in ways that are tied to ecology and diet. In response to the nearly instantaneous processing of returned echoes, sophisticated muscular control can generate rapid changes in pinna directionality and shape. Perhaps the most impressive ears are found in the long-eared bats, such as the Gray Long-eared Bat (*Plecotus austriacus*, page 114), which tucks its long ears under its wings during hibernation to avoid heat loss.

Not surprisingly, the non-echolocating fruit bats and flying foxes in the family Pteropodidae have simple muzzles without nose leaves, no tragus, and moderately sized ears.

← Phyllostomid bats from the tropical Americas emit echolocation calls through their noses; nose leaves act as megaphones for amplifying and directing calls.

A GALLERY OF BAT FACES

The appearance of bat faces varies significantly across the 21 living families. Bat faces may vary with diet, displaying features such as the longer rostrums found in the nectivorous species, or robust jaws found in the carnivores. However, the greatest driver of bat facial features is the type of echolocation calls used, which may or may not be emitted through large nose leaves. The calls emitted vary in frequency and loudness, both of which impact the nature of the returning echoes. The ability to hear and interpret these echoes is in turn tied to the shape of their ears (see page 99).

A. The African Trident Bat (*Triaenops afer*) is in the family Rhinonycteridae, a small family with only nine species, each with modified nose leaves. These bats are closely related to the other Old World nose-leaf bats.

B. The Pallid Bat (*Antrozous pallidus*), like nearly all bats in the family Vespertilionidae, has a simple face and a distinct tragus within their ear.

C. The Northern Little Yellow-eared Bat (*Vampyressa thyone*) is one of the New World leaf-nosed bats, in the family Phyllostomidae.

D. The Pale Spear-nosed Bat (*Phyllostomus discolor*) is also in the family Phyllostomidae. It is common and widespread in Central America and northern South America.

E. The Mauritian Tomb Bat (*Taphozous mauritianus*) is in the family Emballonuridae. Like the bats in the family Vespertilionidae, bats in this family have plain faces and are found in both the New World and the Old World.

F. The Lesser Long-eared Bat (*Nyctophilus geoffroyi*) is also in the family Vespertilionidae, found in Australia and Tasmania. Unusual among the members of this large bat family, it has a unique simplified nose leaf with a Y-shaped groove behind the nostrils.


B

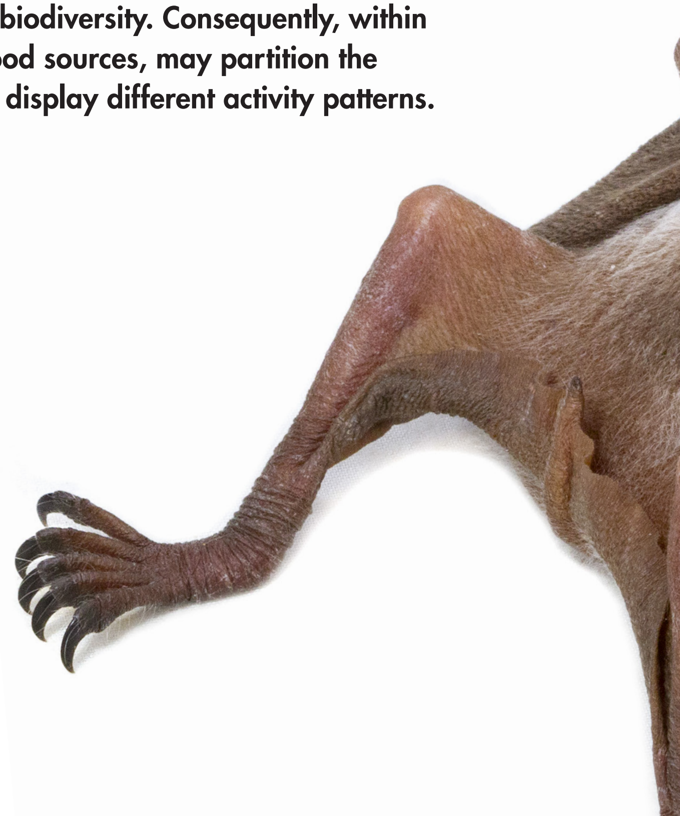

C


E


F

Echolocation and niche partitioning

Natural selection has led competing bat species to exhibit different patterns of resource use, known as niche partitioning. This competition has driven speciation and hence greater bat species biodiversity. Consequently, within a given area, bats may utilize different food sources, may partition the three-dimensional use of space, and may display different activity patterns.



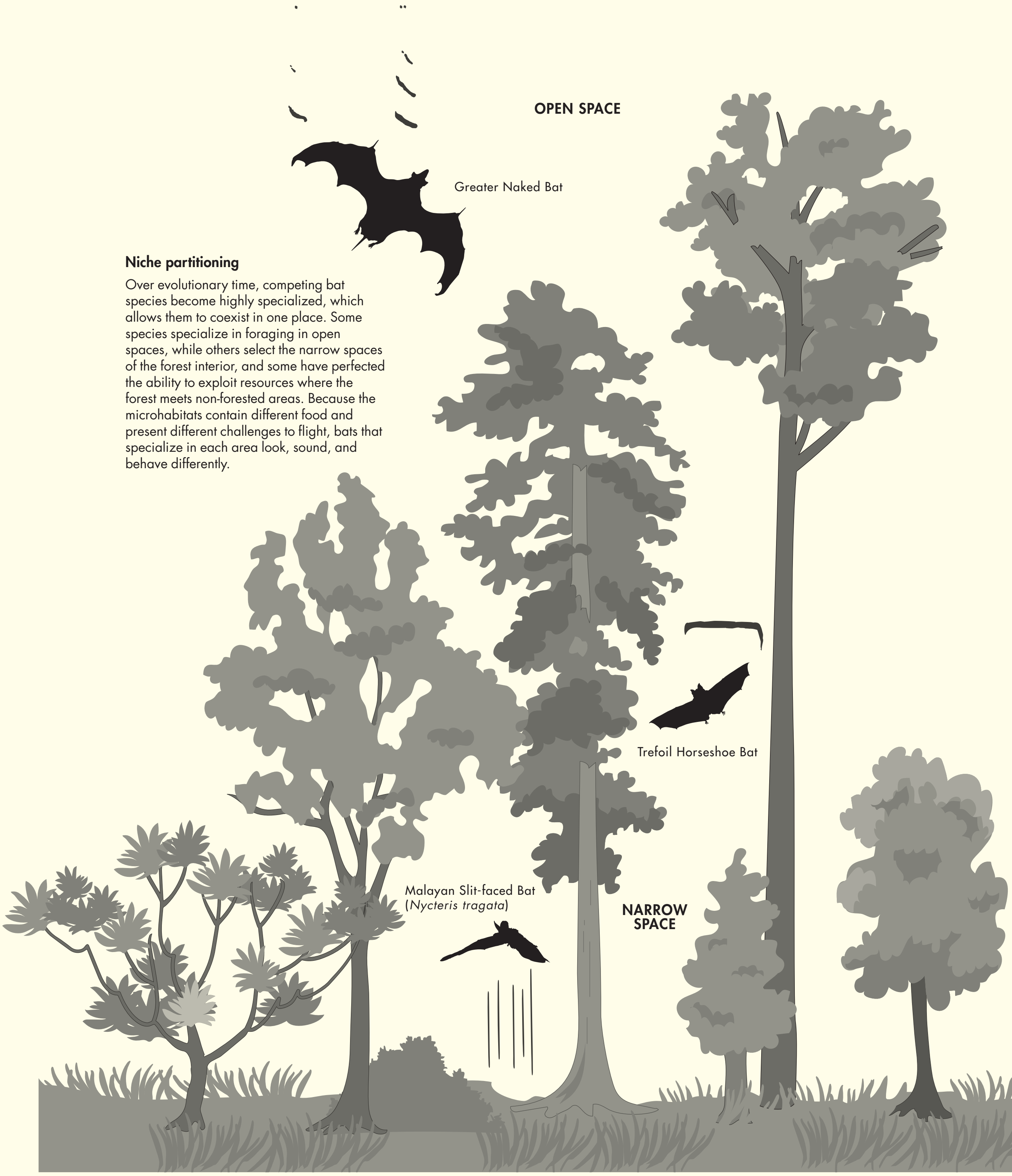
Intricately tied to niche partitioning, species differences in echolocation calls and echolocation patterns are connected to bats' ability to exploit many different types of habitat. Simultaneous selection on wing shape, diet, and echolocation parameters is especially evident in dense tropical forests, in which dozens of bat species have become so specialized that they are able to thrive in the same geographic area (sympatry) with minimal competition (syntopic). A complex form of echolocation called "high duty-cycle echolocation" evolved in the Rhinolophoid bats (the Old World leaf-nosed Rhinolophidae and Hipposideridae) and in several New World bats in the family Mormoopidae, including the Common Mustached Bat (*Pteronotus parnellii*) and its close relatives. This unique strategy enabled detection of flying insects in highly enclosed and clustered environments, which had previously been underutilized niches. Interestingly, the Big Naked-backed Bat (*Pteronotus gymnonotus*), despite being in the same genus as the mustached bats, is not a high-duty cycle echolocator.

The duty cycle of a periodic sound is the proportion of time spent emitting signals. Unlike the majority of echolocating bats that emit a sound pulse and then remain silent while waiting for its echo (low duty-cycle echolocation), bats deploying high duty-cycle echolocation separate pulse and echo information not in time but in frequency. High duty-cycle bats, like the Striped Leaf-nosed Bat (*Macronycteris vittata*) and the Lobed Horseshoe Bat (*Rhinolophus lobatus*) from Africa, largely emit long-duration constant frequency or narrowband calls and have sophisticated neural mechanisms that allow them to specifically detect, lock onto, and track fluttering insects like moths based upon details of the returning echo. They are rarely quiet and interpret returning echoes while simultaneously broadcasting the next call.

↑ The Striped Leaf-nosed Bat is a high duty-cycle echolocator readily identified by patches of white fur on the shoulders, white lateral stripes, and its relatively large size.

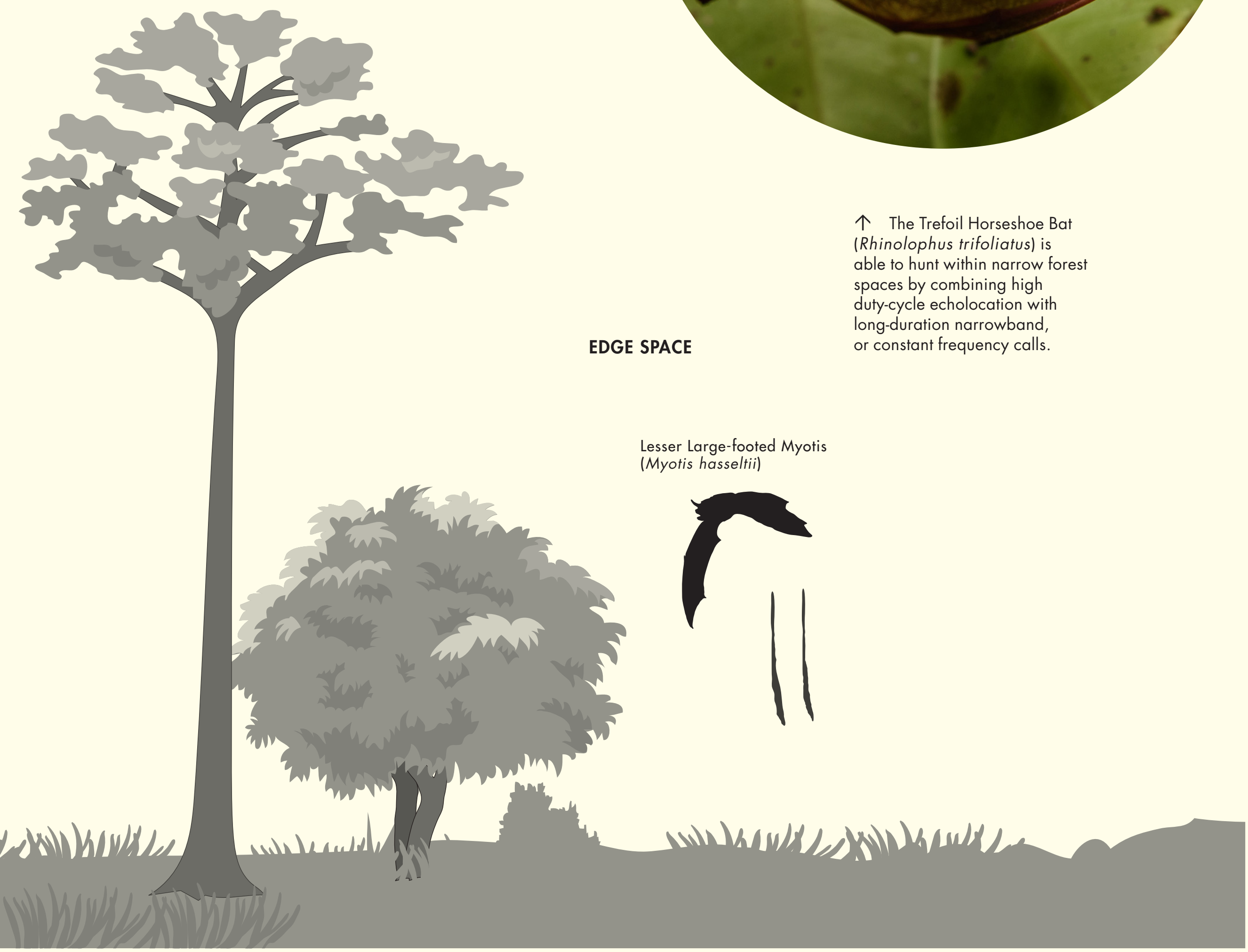
Niche partitioning

Over evolutionary time, competing bat species become highly specialized, which allows them to coexist in one place. Some species specialize in foraging in open spaces, while others select the narrow spaces of the forest interior, and some have perfected the ability to exploit resources where the forest meets non-forested areas. Because the microhabitats contain different food and present different challenges to flight, bats that specialize in each area look, sound, and behave differently.



Bat biodiversity in the tropical forests of Southeast Asia, such as the forests in the Krau Wildlife Reserve, in Peninsular Malaysia, illustrates the effects of natural selection on niche partitioning. Within an area of 1 sq mile (3 sq km), over 50 species of insectivorous bats across seven bat families can be found. Bats in this protected area are segregated by echolocation frequencies and patterns and by size, wing shape, diet, and foraging location, such as open space, including above the tree canopy; edges between forest and open space; and the forest interior—at variable heights between the canopy and the ground.

↑ The Trefoil Horseshoe Bat (*Rhinolophus trifoliatus*) is able to hunt within narrow forest spaces by combining high duty-cycle echolocation with long-duration narrowband, or constant frequency calls.

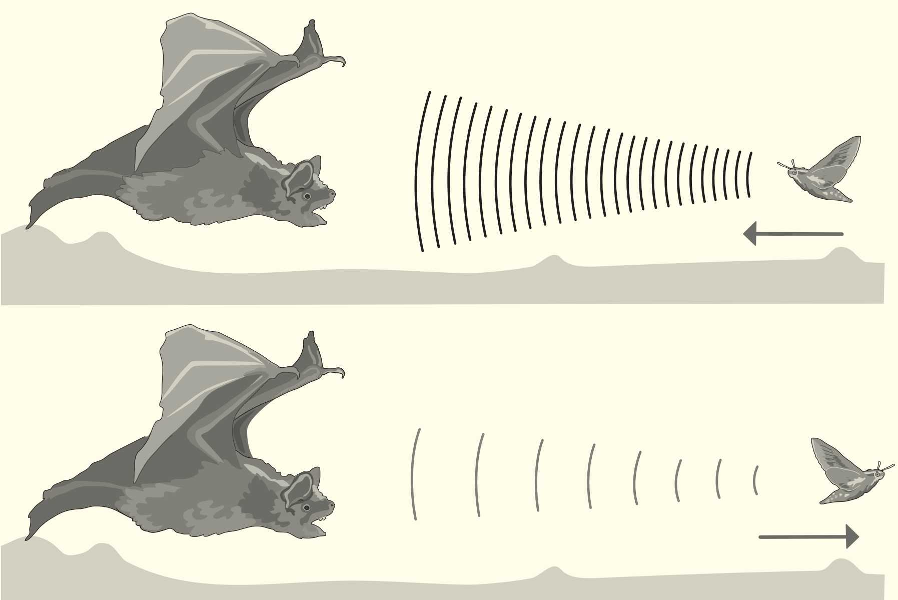


Moths versus bats

The ultimate predator–prey relationship within Chiroptera is the global hunting of moths by bats. Indeed, a coevolutionary arms race has been waged between bats and moths for millions of years. Bats evolved precise and complex mechanisms to efficiently hunt moths, even those found in highly cluttered forest interiors. Moths, in turn, have devised a number of ingenious strategies to avoid predation.

One of the greatest challenges for identifying moving prey by echolocation is the Doppler effect. The most familiar example to help understand this is the way in which the sound of an ambulance siren changes—as it approaches the siren sounds higher pitched, but when it passes and recedes it suddenly sounds lower. As the vehicle approaches, sound waves are pushed against your ears and are compressed like a spring. This decreases the wavelength, which increases the frequency, and hence the pitch of the sound. The change in pitch is directly related to the speed at which the source is moving and thus can be interpreted by the brain to determine distance and direction.

In the case of bats, the sound waves in question are the returning echoes of a flying moth or other insect. If the prey item and the bat are stationary, the echoes return with consistency. If, however, the moth is flying toward the bat (and/or the bat toward the moth), and thus the distance between them is shortening, returning echoes increase in frequency relative to the combined



Doppler effect

Some bat species are able to perceive increases in frequency (top) and decreases in frequency (bottom) and interpret whether prey are moving closer or farther away.

speeds of the bat and insect. Bats, especially those that use high duty-cycle echolocation, make use of the Doppler shift to calculate speed and thus distance relative to the objects around them. These bats, in which moth consumption is especially high, display "Doppler-shift compensatory behavior"; species like the Rufous Horseshoe Bat (*Rhinolophus rouxii*) alter the frequency of their echolocation calls to compensate for the Doppler shifts in returning echoes.

Bats can also take advantage of small shifts in returning echoes generated by the wing movement of moths. As echolocation calls bounce off moving moth wings they produce high-intensity (louder) echoes, called "acoustic glints." Bats can interpret these glints to determine directionality of moth flight and thus better hone in on the location of their prey. Such echolocation super skills make these bats exceptionally good at locating fluttering targets in cluttered environments.

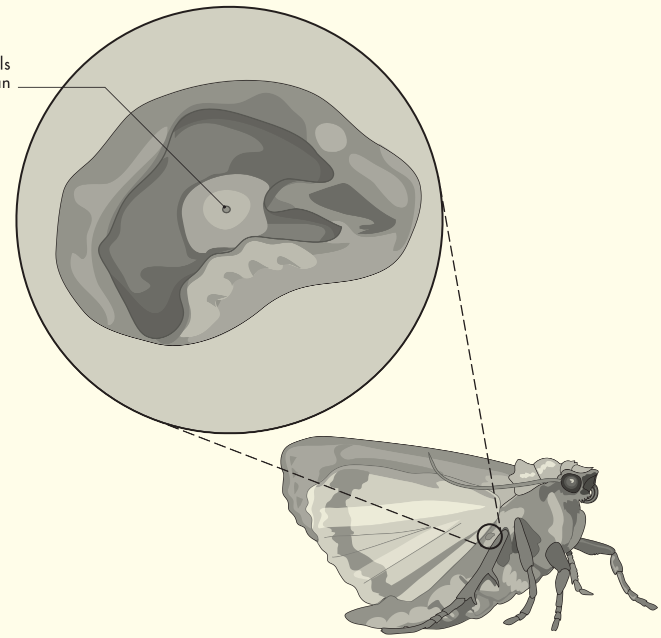
↑ The Rufous Horseshoe Bat can neurologically account for the Doppler shift, improving its hunting precision.

HOW MOTHS FIGHT BACK

Not surprisingly, moths have fought back, evolving counter-sonic mechanisms to avoid bat predation. The first of these is fine-tuning of their hearing. Moths (and other insect taxa) have evolved "tympanic organs" that are specifically and exceptionally sensitive to the ultrasonic frequencies of the bats with which they have coevolved. As a result, moths, listening only for bat calls, can detect bat predators at approximately 65–320 ft (20–100 m), whereas bats can only detect moths at 3–30 ft (1–10 m).

The second counterstrategy used by moths is acoustic aposematism: some moths produce ultrasonic sounds to warn bats of their noxious taste. Although we are most familiar with visual aposematism, such as the bright orange wings with black variegation on monarch butterflies, moths also advertise unpalatability to potential predators through sounds, and bats learn to avoid them. Other moths deploy Batesian mimicry, producing warning sounds similar to those of noxious moth species, even though they themselves are otherwise perfectly edible. A 2022 study of over 250 moth genera from around the world found frequent evidence for acoustic warning and mimicry and suggested that they are the *raison d'être* for sound production in most moths, which are otherwise generally silent.

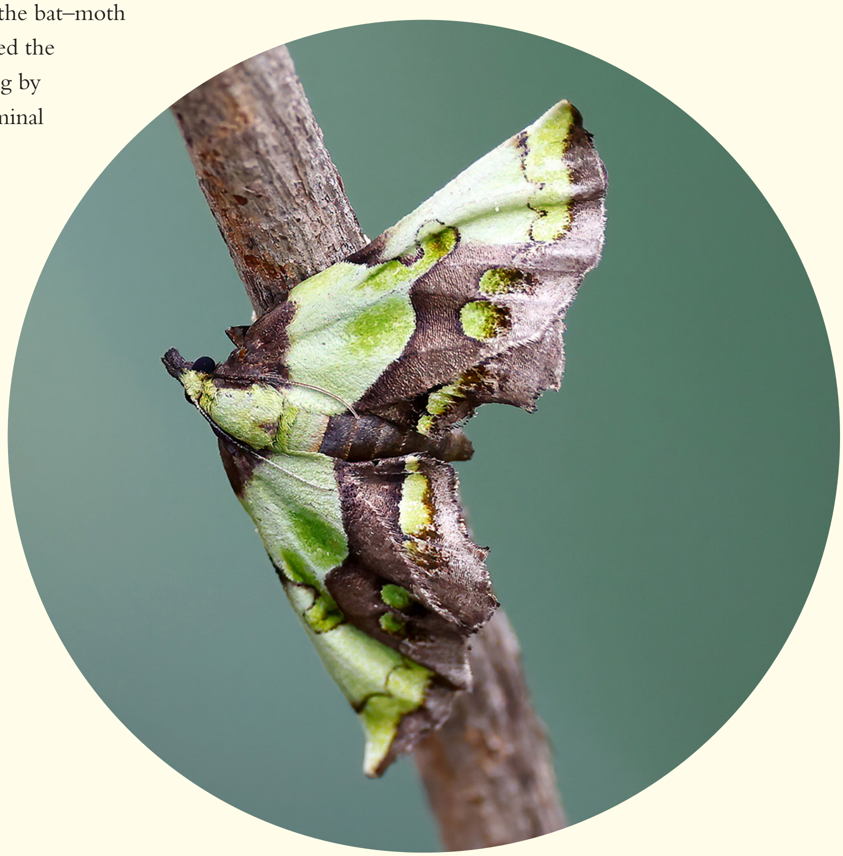
Moths can produce sound in several ways: abdominal stridulation, percussive wing beating, and tymbals. These sound-producing organs not only serve



Moth ear

Typanic organs are located in various parts of the insect body, including the thorax, abdomen, and mouthparts.

to warn bats, but are also used by some moth species to deploy the third and perhaps most sophisticated type of anti-bat strategy: the jamming of bat sonar at the critical final phase of the hunt. This highly effective emittance of high-duty cycle ultrasound interferes with the bat's hearing and its ability to discriminate target distance, and has evolved independently within moths at least six times. Not to be undone in the bat–moth arms race, at least some bats have evolved the ability to compensate for sonar jamming by extending the duration of the final terminal echolocation buzz and thus overcome the moth's attempt to save itself.



↖ Nearly all bat families contain bat species that hunt moths, including this Brown Long-eared Bat, in the family Vespertilionidae.

→ The moth species *Mittonia hampsoni* produces ultrasonic sounds in response to bat echolocation calls. It does this using the unique mechanism of beating its wings against its tegula (a small abdominal structure) in flight.

EPTESICUS FUSCUS

Big Brown Bat

Frequently roosts in human-made structures

SCIENTIFIC NAME	*Eptesicus fuscus*
FAMILY	Vespertilionidae
DIET	Beetles and other hard-bodied insects
HABITAT	Forests and caves, but often roosts in human-made structures
CONSERVATION STATUS	Least Concern
WEIGHT	0.39–0.81 oz (11–23 g)
WINGSPAN	12.8–13.8 in (32.5–35.0 cm)

Big Brown Bats are one of the most common species in North America, in part due to their physiological tolerance of a variety of environmental conditions. This hearty bat is relatively small, with long, silky, brown fur and a tail fully enclosed in the wing membrane.

Populations of Big Brown Bats may have increased in recent decades due to an increased availability of human-made structures that can be used as roost sites. During the summer or active season, female bats and their pups often form large maternity colonies in barns and attics. These colonies can range from a handful to hundreds of bats. Males roost alone or in small groups, joining the females again later in the summer. Most Big Brown Bats in the northern regions of their range will migrate to winter roost sites, where they mate before entering the cave or mine to hibernate. If they do not accumulate sufficient fat stores before hibernation, young bats will die during their first winter.

Unlike many other North American bat species that hibernate, Big Brown Bats are resistant to the pathogen that causes the deadly bat disease known as White-nose Syndrome (see page 222). This, combined with their higher reproductive rate of two pups per year in some parts of North America, has made them the most common bat encountered in much of the United States. A resilient species that does well in captivity, Big Brown Bats have been studied for a variety of reasons and played an important role in our understanding of how echolocation works.

→ Big Brown Bats are evolutionary champions. They are disease-resistant, adaptable, and master hunters.

PHYLLONYCTERIS POEYI

Cuban Flower Bat

Hot cave rooster

SCIENTIFIC NAME	*Phyllonycteris poeyi*
FAMILY	Phyllostomidae
DIET	Pollen and nectar, occasionally fruit and insects
HABITAT	Varied, both xeric and mesic
CONSERVATION STATUS	Least Concern
WEIGHT	0.5–1.0 oz (15–29 g)
WINGSPAN	11.6–13.8 in (29.4–35.0 cm)

With its long, narrow snout, the Cuban Flower Bat is an important pollinator that also consumes nectar, fruit, and the occasional insect found incidentally on the large flowers from which it feeds.

The medium-sized Cuban Flower Bat has short, thick fur with bicolored hair which is white at the base and grayish-brown at the tips. Males are slightly larger than females on average. This species is not capable of hovering flight and, with its relatively large feet, lands on flowers when feeding rather than hovering. Its echolocation call is unique—long, intense, narrowband calls maximize their flower-detecting range.

The Cuban Flower Bat has a restricted distribution, being found only on the islands of Cuba and Hispaniola. Inhabiting xeric (dry) and mesic (moderately moist) habitats from sea level up to 5,600 ft (1,700 m), this species is very abundant within its range. This bat is unusual in that it preferentially and exclusively roosts in hot caves. Within these sites, Cuban Flower Bats select the warmest locations. They have been recorded roosting at temperatures up to 104°F (40°C). This exceptionally gregarious bat roosts in colonies of several thousand to several hundred thousand bats. In fact, their presence in such high numbers further elevates the temperature within the cave. Although they may share their cave roosts with other bat species, they separate themselves by species within the cave.

Females bear a single pup each summer and leave them in the cave while foraging. When the moon is full most bats remain in the roost rather than emerging to feed, presumably due to increased predation risk.

→ The Cuban Flower Bat's fur becomes covered in pollen as it feeds. It then transfers this pollen as it moves from flower to flower.

PLECOTUS AUSTRIACUS

Gray Long-eared Bat

Quiet listener

SCIENTIFIC NAME	*Plecotus austriacus*
FAMILY	Vespertilionidae
DIET	Moths
HABITAT	Varied, from forests to urban areas
CONSERVATION STATUS	Near Threatened
WEIGHT	0.21–0.35 oz (6–10 g)
WINGSPAN	10–11.8 in (25.5–30.0 cm)

The Gray Long-eared Bat is distinguished by its fur color and by the long, broad, dark-colored tragus within the ear, which allows it to vertically discriminate objects in three-dimensional space.

The Gray Long-eared Bat is endemic to Europe, where it is widely distributed; it has also colonized several Mediterranean islands. This hibernating species occupies multiple habitat niches, with populations found from lowland valleys and grasslands to high mountain pastures or woodlands. Although this bat normally roosts in hollow trees or caves, it readily adapts to the urban environment and can be found in houses, roofs, castles, churches, and bat boxes.

Populations of Gray Long-eared Bats are declining across most of its distribution due to intensive agriculture and land conversion, leading to fewer available roosts and insects. In Germany, declines have been tied to the use of pesticides. This is a relatively sedentary species, which typically only travels approximately 3 miles (5 km) per night and hibernates close to its summer roosts.

Long-eared Bats emit quiet echolocation calls, potentially through both their mouth and nose. Their low-intensity calls make acoustic monitoring of populations with specialized "bat detectors" (that record calls and identify species) difficult. Although the long-eared bats generally hunt by gleaning prey that are not moving, this species also appears to hunt flying prey. Like other long-eared bats, it may sometimes hunt visually and may rely on prey-generated sounds to detect moths, their primary diet. The need to detect the quiet echoes that return from their calls and to detect the sounds of prey explain the size of the ears in this unique bat lineage.

→ The Gray Long-eared Bat's relatively large eyes and exceptionally large ears help it hunt moths that are quietly hiding and not in flight.

PTERONOTUS MESOAMERICANUS

Mesoamerican Mustached Bat

Funnel faced

SCIENTIFIC NAME	*Pteronotus mesoamericanus*
FAMILY	Mormoopidae
DIET	Beetles, moths, and other insects
HABITAT	Varied, multiple types of tropical forests and arid regions
CONSERVATION STATUS	Least Concern
WEIGHT	0.56–0.67 oz (16–19 g)
WINGSPAN	Not known

The most striking feature of the Mustached and Naked-backed Bats in the family Mormoopidae is their modified lips, which form a funnel or megaphone-like structure during flight, likely focusing and amplifying their echolocation calls.

The Mesoamerican Mustached Bat was originally considered a subspecies of the Common Mustached Bat (*Peteronotus parnelii*), the only New World Bat thought to use high duty-cycle echolocation. However, recent analyses of skull morphology and DNA sequences revealed that the Common Mustached Bat actually contains a number of taxa. Multiple species, including the Mesoamerican Mustached Bat, are now recognized. With their funnel-shaped lips, this species emits high-intensity (loud) calls that consist of long constant-frequency (CF) components.

Mesoamerican Mustached Bats are restricted to Central America, where they are widespread. They occupy a variety of habitats, ranging from humid to arid and from coastal lowlands to montane forests—up to 7,200 ft (2,200 m) in elevation. During the day, Mesoamerican Mustached Bats prefer to roost in the largest chambers of hot and humid tropical caves. Female Mesoamerican Mustached Bats form large maternity colonies and give birth to a single pup each year. The fur of this species can vary from dark brown to orangish, with an abdomen that is lighter than the back. An albino individual was captured in Mexico and alopecia, or the loss of fur from stress or poor health, has also been documented in this species.

Mesoamerican Mustached Bats consume a variety of arthropods, including beetles, moths, and flies. Interestingly, subtle but significant individual variation in wing shape in this species is tied to diet, most likely through the relationship of wing shape with foraging efficiency. Individual bats with more rounded and broader wings, which translate to greater maneuverability, feed on a greater range of arthropods than do bats with pointed and more triangular wings.

→ Like other Mormoopid bat species, the Mesoamerican Mustached Bat has relatively broad wings and a squared-off uropatagium.

DIET

A varied diet

The ancestral bat, like ancestral early mammals, was most likely an insect eater. The majority of bats alive today still consume insects, but significant numbers of bats feed on other arthropods, vertebrates (including mammals, birds, reptiles, and amphibians), and multiple types of plant material, such as fruit, nectar, and pollen.

Nocturnal insects are plentiful and bats have few competitors for this abundant food source. The dietary diversity provided by insects, along with diets containing other arthropods, vertebrates, and energy-rich plant material, has played a significant role in the evolution of bats, and is partly responsible for the morphological, physiological, and ecological diversity we see today.

Arthropods are the largest animal phylum, constituting approximately 80 percent of all known living animals. The majority of described arthropods are insects and about 70 percent of all bat species are classified as "insectivorous," a catchall term that generally includes other arthropods as well. Indeed, some bats have highly specialized diets that may include other arthropods such as spiders, scorpions, centipedes, and even aquatic invertebrates like crustaceans. For example, the Pallid Bat (*Antrozous pallidus*, page 144) from North and Central America, which feeds on arthropods like crickets and spiders, and occasionally nectar and pollen, is renowned for its ability to consume Arizona bark scorpions (*Centruroides sculpturatus*), the most venomous scorpions in North America, to whose venom they are immune.

The Pallid Bat, like other bats that catch larger arthropod prey, is a gleaner, plucking its prey directly from surfaces. On the other side of the world, bats in the family Nycteridae, such as the Egyptian Slit-faced Bat (*Nycteris thebaica*, page 142), also glean arthropods from the ground or low foliage. They detect the rustling sounds of moths, beetles, and orthopterans (grasshoppers, locusts, and crickets) and then use low-intensity (quiet) echolocation calls to locate them and pluck them from their stationary position. Among insectivorous bats, these gleaners are less common as most insect eaters catch their prey "on the wing," a feeding strategy called aerial hawking. This sophisticated hunting of mobile prey is made possible by remarkable echolocation and maneuvering.

← The Pallid Bat is renowned for its ability to hunt and consume scorpions, although it also feeds on crickets, spiders, and even nectar and pollen.

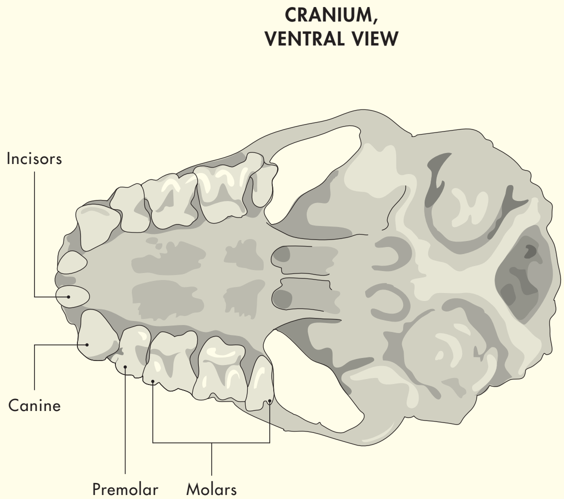
↑ The Brown Long-eared Bat, seen here eating a moth, is a well-studied European insectivorous bat.

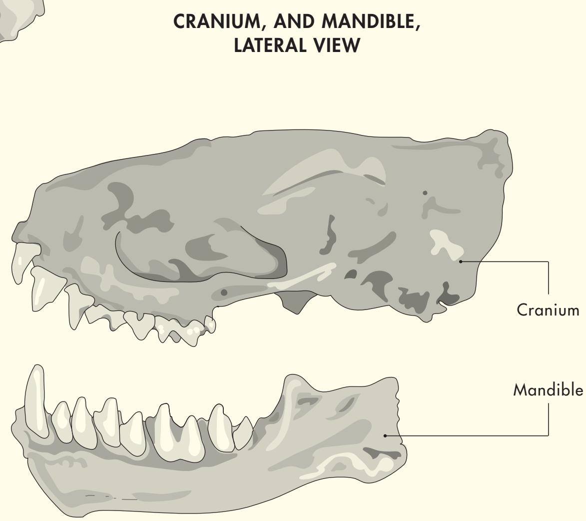
INSECTIVOROUS BATS

Based mostly upon the shape of their teeth, ancestral bats were nearly certainly insect eaters. Insectivorous bats alive today have between 28 and 36 teeth, which are collectively one of their heaviest skeletal elements. The robustness of bat teeth, inherited from their non-bat mammal ancestors, is necessary for their diet and has ensured that teeth are well preserved in fossils. Indeed, most bat fossils consist solely of isolated teeth, given that the otherwise delicate bat skeleton does not fossilize well.

Insectivorous bats typically have sharp, pointed incisors and canines which they use for seizing and holding onto prey. For bats that eat hard-bodied insects like beetles, these teeth are especially robust. Coupled with strong jawbones and large jaw muscles, they facilitate the puncturing and crushing of the insect's hard chitinous exoskeleton. Behind their canine teeth, bats have variable numbers of premolars and molars (the latter being distinguished by not having a deciduous precursor—that is, a "baby tooth" which is later replaced). These teeth are also sharp and highly pointed in insect-eating bats.

Both ancient and extant insectivorous bats are generally relatively small, at least compared to modern bats that eat other types of prey. Bats are small mammals and fly for hours upon hours each night, so they have exceptionally high energy needs. These needs can only be met with energy-rich food, usually in the form of the protein and fat found in insects, which also supply fiber, minerals, and vitamins.





Bat skull and teeth

Bat skulls and teeth are robust and heavy. Note the height of the cusps on the teeth of this White-bellied Free-tailed Bat (*Mops niveiventer*).

↑ The Particolored Bat (*Vespertilio murinus*), like other insect specialists, has many sharp teeth for grasping, holding, and crushing arthropods. Similar to other vespertilionid bats, it has a large gap between its two front incisors.

Although some non-flying (and much larger) mammals like koalas, elephants, buffalo, and some primates can subsist on the relatively poor nutrient and energy content found in leaves and other vegetative plant parts, there are no bats that survive only on leaves. Bats need high-quality food and lots of it, typically consuming 50 percent or more of their own body weight in insects each night. To put this in perspective, for the average human, weighing 136 lb (62 kg), the comparable nightly diet would be 4.25 lb (2 kg) of animal protein (more than 200 hamburgers' worth).

DIETARY DIVERSIFICATION

Some bats meet their dietary requirements through highly specialized diets in which they focus on a single or small number of specific prey species hunted with optimal precision. For example, Underwood's Bonneted Bat (*Eumops underwoodi*) specializes in hard-bodied insects, primarily beetles. Other insectivorous bats are more opportunistic, eating what is most easily available rather than investing time searching for very specific prey. Dietary specialization, discovered through molecular and morphological analysis of gut contents or bat feces, is one mechanism through which bats partition niches in resource-rich environments, leading to the diversification into multiple species. Although multiple examples of diet-driven speciation appear within the various lineages of insect-eating bats, the convergent adoption of other feeding modalities in multiple bat lineages further drove bat diversity and the ability of bats to live and eat in new environments.

This adaptive dietary radiation is best exemplified by the New World bats in the family Phyllostomidae. Adaptive radiation, like that demonstrated by Darwin's finches, is an evolutionary process in which a single ancestor species rapidly diversifies into a wide array of forms, often adapting to different ecological (including dietary) niches or environmental conditions. The diverse phyllostomid lineage of "whispering" and gleaning leaf-nosed bats, with 230 species to date, has greater morphological and ecological diversity than any other bat group—including the largest bat family, Vespertilionidae, which has over 533 bat species.

Phyllostomid bats exploit multiple food sources across various habitat types, including lowland tropical rain and dry forests, cool montane forests, and semiarid

deserts. They roost in caves, trees, and human-made buildings, and even make their own tents. Some are fruit eaters, some specialize on nectar and pollen, some eat insects. Still others eat small vertebrates, including birds, lizards, frogs, and mammals. The three species of sanguivorous bats (the vampire bats), which are highly specialized to feed only on blood, are also found in this megadiverse family.

Although scientists like to categorize animals by their feeding ecology, we are discovering that many bats have much more dietary flexibility than previously thought. Some, like the Greater Spear-nosed Bat (*Phyllostomus hastatus*), one of the phyllostomids, can even be considered opportunistic omnivores; these bats are known to consume fruit, pollen, insects, bats, mice, and birds. Keeping in mind their exceptionally high energy needs, it is no surprise that bats will sometimes eat whatever is available.

↖ The White-throated Round-eared Bat (*Lophostoma silvicola*) is known for its consumption of katydids in Pacific and Caribbean lowlands, but also eats other insects, whip scorpions, and fruit.

↑ An opportunistic omnivore, Greater Spear-nosed Bats are known to eat just about anything, including other bats, birds, and rodents, but also fruit, pollen, and insects.

Fruit, nectar, and pollen eaters

High-energy food can be obtained not just from animal protein, but also from the reproductive parts of plants. Unlike insects and other animal prey, fruit, nectar, and pollen do not give chase or emit sounds that give away their location. Bats that specialize on these calorie-dense plant parts have a variety of adaptations to locate their plant prey, using vision, smell, and in some cases echolocation.

Frugivory is largely the domain of two bat lineages: the Old World fruit bats in the family Pteropodidae and several subfamilies within the dietarily diverse New World Phyllostomidae (leaf-nosed bats). Fruit bats, like the Spectacled Flying Fox (*Pteropus conspicillatus*, page 148), have retained large canines, which are useful for grasping and carrying fruit. In fact, flying foxes, which are the largest of bats, have such big canine teeth that they are used as currency in the Solomon Islands. The premolars and molars of bats that mostly or exclusively eat fruit have more rounded cusps compared to bats that primarily eat insects. These cheek teeth are used for crushing fruits.

← The Silky Short-tailed Bat (*Carollia brevicauda*) is one of the most numerous bats in lowland rainforests. Primarily a fruit-eating bat, it will also occasionally eat insects.

↗ Seba's Short-tailed Bat visits a variety of fruits and flowers. Olfactory cues help it determine when nectar and fruit are available.

Many fruit-eating species also have ridges on their palate which they use as "juicers." By pressing their muscular tongues against these ridges, they can squeeze pulp from fruit and then spit out the pellet of plant fiber.

The pteropodid fruit bats, with over 202 species, do not use laryngeal echolocation and the few that echolocate with tongue-clicks or wing claps largely do so to navigate within caves. Instead, they search for food with their excellent dichromatic vision (they can see in two colors). In fact, their large, sensitive eyes, combined with a simple muzzle and ears and elongated rostrum, are responsible for their "fox-like" appearance. The phyllostomid fruit-eating bats have relatively large eyes but not nearly as large as the Old World fruit bats. Phyllostomid fruit-eating bats like the Jamaican Fruit-eating Bat (*Artibeus jamaicensis*) and Seba's Short-tailed Bat (*Carollia perspicillata*) rely on vision and laryngeal echolocation for navigation. Unlike some of the phyllostomids, the Old World fruit bats cannot hover in flight and must either land near the fruit source or quickly grab a piece of fruit for the ultimate takeout dinner. All frugivorous bats identify ripe fruits from their smell, which travels through the air in odor gradients, allowing bats to home in on their location. Bats also remember the location of fruit trees from year to year. Bats that eat coarser, less easily accessed fruit have improved biting performance compared to those that consume soft, fleshy fruit.

← The Dagger-toothed Long-nosed Fruit Bat (*Macroglossus minimus*) is an Old World fruit bat that cannot hover, and must land on flowers in order to reach the nectar inside.

→ Some New World fruit bats are capable of hovering flight and can easily approach and feed while flying, like this Mordant Nectar Bat (*Lonchophylla mordax*).

EATING NECTAR AND POLLEN

The consumption of flower nectar (and occasionally pollen) arose independently several times within the Old World and New World fruit bat lineages. Nectar is an excellent source of sugar, but also rich in lipids, whereas pollen is rich in protein. Natural selection has led to longer narrow muzzles and fewer, smaller teeth in nectarivorous bats—optimized for reaching deep into the base of flowers where nectar is found.

Bat-pollinated flowers are generally large, pale in color, open at night, and have a strong odor. They produce copious amounts of nectar to encourage their bat friends. Similar to fruit, which exists to be eaten by animals that will disperse its seeds, nectar is essentially a bribe from the plant to its pollinators. Nectar makes up about 75 percent of the diet of the Lesser Long-nosed Bat (page 146), which also consumes pollen. As it feeds, the hair on its head and shoulders gathers pollen, some of which is deposited on the flowers of neighboring plants. Some "chiropterophilic" flowers in the New World, which have coevolved with their echolocating phyllostomid bat pollinators, serve as acoustic beacons. When in full bloom and full of nectar, their particular shapes absorb and/or reflect echolocation signals such that bats can readily detect and target them, ensuring a meal. This coevolutionary dance is similar to that seen between flowers and other pollinators, such as bees and hummingbirds, in which flower morphology and scent are fine-tuned to attract their animal pollinators.

As described earlier, nectar-feeding phyllostomid bats are adept at hovering flight, maintaining a stable position from which to extract nectar from flowers. Bats can consume up to five times their weight each night and will select nectar with the highest sugar content. Specialized digestive adaptations allow some nectar feeders, like Pallas's Long-tongued Bat (*Glossophaga soricina*), to fuel nearly 80 percent of the cost of hovering with just-ingested sugar. Not surprisingly, nectar-feeding bats have long tongues that may be flexible and modified to soak up nectar. For example, the Lesser Long-nosed Bat has brush-shaped, elongated papillae (little extensions) at the tip of its tongue which help "mop" nectar from inside flowers.

The vampires

Many invertebrates, such as ticks, fleas, bedbugs, mosquitos, leeches, and tsetse flies, survive on a blood-meal diet, but the three species of vampire bats are the only vertebrates to exclusively exploit this protein-rich food source.

Legends of vampirism exist from many cultures and predate the scientific discovery of vampire bats by thousands of years. The three vampire bat species alive today are sister taxa and the only extant members of the subfamily Desmodontinae, within the Phyllostomidae. The White-winged Vampire Bat (*Diaemus youngii*) and the Hairy-legged Vampire Bat (*Diphylla ecaudata*) are less frequently encountered than the abundant Common Vampire Bat (*Desmodus rotundus*), which has the greatest geographic range and is found in greater numbers. This species, unlike the others, prefers mammals and is widespread in tropical and subtropical regions of the New World, extending just into the southern United States. It appears to prefer hunting large mammal prey, and thus the introduction of domestic cattle, pigs, and horses to the New World has likely led to dramatically increased population numbers over the past few centuries. Of all of the bat species in which full dietary diversity has been studied, only vampire bats are dietary purists.

Blood is a rich source of energy, but surviving only on blood as an adult requires a number of specialized behavioral, morphological, and physiological adaptations. Prey are located using multiple senses, including smell, passive listening for the deep breathing sounds of sleeping prey, and echolocation. Vampire bats are unusual in how well and how quickly they move on the ground, loping and jumping by anchoring their hind feet and extending their robust wrists forward. After firmly planting their wrists, they bring their hind feet and bodies forward, completing the stride.

Highly specialized, heat-sensing pits near the bat's nose allow them to locate capillary-rich areas of skin. Once a site is identified, specialized cheek teeth in both the upper and lower jaw, along with sharp canine teeth, are used to clip away feathers and fur. All three vampire species then initiate the blood meal with a feeding bite, in which a tiny piece of the victim's skin is removed. Blood flows from the small wound created by their enlarged, blade-like upper incisors.

← The White-winged Vampire Bat is found from Mexico to Northern Argentina and is present on the islands of Margarita and Trinidad.

↑ Wild birds are the preferred food source for the Hairy-legged Vampire Bat but they will also readily feed on domestic poultry, like this chicken.

← After making a quick cut with their blade-like incisors, Common Vampire Bats use their tongues to lap up their meal. Their tongues have lateral grooves in them that channel the blood and allow them to consume large quantities.

→ Common Vampire Bats can be seen emerging from their roosts in hollow trees, where they congregate in social groups.

RECIPROCAL ALTRUISM

Vampire bats that miss a nightly meal are at risk of starvation, yet we know that not all bats forage successfully each night. In fact, adults may miss an average of one night per month, while younger, less experienced animals may miss a meal several times per week. A unique system has evolved within vampire social systems in which successful bats, after returning to the roost, will regurgitate part of their blood meal to feed a bat that failed to find prey. This altruistic act is not random, however, as bats appear to form long-term, cooperative relationships, even with non-kin. These reciprocal, tit-for-tat relationships ensure that freeloaders are not rewarded. In fact, previous meal sharing from bat A to bat B is a better predictor of subsequent meal sharing from bat B to bat A than is kinship.

In a recent landmark study, how these relationships are formed in the first place was studied in non-related vampires who did not know each other previously. Like many other social animals, vampire bats display social grooming, in which they lick the fur and wings of other bats. Researchers found that bats slowly formed new relationships through mutual social grooming. This low-cost activity effectively allowed them to "test the water" or strength of their relationship prior to the more costly behavior of sharing a previous blood meal. In fact, bats that groomed each other at high rates were more likely to reciprocally donate food. Whether these relationships go beyond scorekeeping to something akin to "friendship" remains an intriguing, yet unanswered question.

BLOOD AS A FOOD SOURCE

Bats overcome the victim's blood-clotting mechanism by including an anticoagulant agent in their saliva, which also acts as a local vasodilator—together maintaining a steady flow of blood that the bat laps up. The Common Vampire Bat, which weighs 1–1.25 oz (30–35 g), will consume approximately 0.88 oz (25 g) of blood over a 20–30 minute period. They are in fact so heavy post meal (hence the Latin name "*rotundus*") that they must digest their blood meal before they can fly. Using highly efficient kidneys, they rapidly extract the fluid portion of the blood meal (plasma) and excrete it as urine, even while the meal is progressing.

The bat carnivores

Bat carnivory, the hunting and consumption of other small vertebrate animals, is an evolutionary extension of insectivory. It has convergently evolved in a handful of bat lineages around the world. Carnivorous bats, which often still consume arthropods, are generally larger than typical insectivores. Some catch birds or fish on the wing, but most carnivorous bats are gleaners, hunting stationary prey.

Both insects and vertebrate animal flesh provide high-energy protein. With increased body size, bats have expanded into the ecological niche afforded by larger animal prey. Indeed, the two largest bats that are not in the family Pteropodidae (which includes the very large flying foxes) are both carnivorous. The Spectral Bat (*Vampyrum spectrum*), from the megadiverse Phyllostomidae, is exceptionally large, with a wingspan of nearly 1 yard (1 m) and a mass of up to 6.7 oz (190 g). Like other carnivores, it is a versatile predator, hunting birds, bats, rodents, and insects. In a spectacular example of convergent evolution, another very large carnivore is found in Australia: the Australian False Vampire Bat (*Macroderma gigas*). This bat has some of the most sensitive hearing of any bat studied and relies on prey-generated sounds to locate its victims. In these two bat species and others around the world known to eat small vertebrates, little modification of the sharply cusped ancestral insectivore teeth was necessary.

→ The Australian False Vampire Bat is a fearsome predator, weighing in at up to 6 oz (170 g). It returns to its perch to consume its meals.

TRAWLING

Trawling is a particular hunting strategy in which bats hunt over still water and use their feet to take prey from the surface. Bats typically fly just above the water surface and modify their wingbeats, so as to not dip the tips of their wings in the water. Although many trawlers are catching emerging insects, the Greater Bulldog Bat and the Fish-eating Myotis have expanded their diet to include fish. These neotropical bats have long legs and huge feet with long, sharp claws. Their wings have a high aspect ratio and low wing loading. Their efficient yet powerful flight is aided by the ground effect in which the flat water surface acts as an aerodynamic "mirror," increasing the air pressure between the water surface and the wing, generating lift.

→ A sequence showing a successful trawling expedition (in this case for an insect) by a Greater Bulldog Bat.

Ecosystem services

What would life be like without bats? Bats play critical roles in diverse ecosystems around the world. They control insect populations, disperse seeds, pollinate flowers, and provide rich fertilizer for forests and cave ecosystems. Their contributions also extend to us: providing ecosystem services that benefit human well-being.

Bats, through their roosting and foraging ecologies, contribute significantly to the global balance of nature. With their exceptionally high energy needs, bats are major consumers of insects and fruit and also play roles in regulating the populations of other vertebrate and invertebrate animals. Bats impact ecosystems both directly and indirectly, affecting the survival and quality of life for Earth's human and nonhuman inhabitants.

The most frequently described benefits arise from the role bats play in regulating insect populations since they frequently consume arthropods that are considered pests. For example, in Brazil, the larval stage of the Fall Armyworm Moth (*Spodoptera frugiperda*) is a major pest of maize. Multiple bat species prey on the adult moths, thereby suppressing populations. Researchers estimate that the hunting of these pests by bats saves Brazilian farmers US $390.6 million per harvest. In the United States, the total annual dollar value of pest suppression by bats and avoided pesticide use is estimated at $23 billion per year.

← The Fall Armyworm Moth is a major agricultural pest that is spreading globally. Bats significantly control these pest populations, avoiding millions of dollars in crop losses annually.

↗ The Great Fruit-eating Bat (*Artibeus lituratus*) can carry way heavy fruits after extracting them from the tree. Seeds that pass through its gut will regenerate forests some distance away.

Most flowering plants cannot successfully reproduce without animal pollinators. Nectar-feeding bats are dusted with pollen while feeding and transfer pollen to other plants. Although bees and birds are more important pollinators, bats pollinate hundreds of plant species, including a surprising number of economically and ecologically important plants. For example, bats pollinate the flowers of the blue agave (*Agave tequilana*), from which commercial tequila is distilled in Mexico and neighboring regions. Overall, bats pollinate a dizzying array of native and commercial plants, including bananas, breadfruits, figs, durians, cashews, and mangos, as well as the shea tree (from which we obtain shea butter) and related trees. Finally, frugivorous bats disperse seeds across great distances, regenerating forests, including those destroyed by human activities. Although financial estimates of the value of bat activities for humans are challenging to calculate, the critical role of bats in both pristine and altered habitats is undisputed.

↑ Old World Fruit Bats, such as this Spectacled Flying Fox, consume many native fruits and thus help restore damaged habitats.

↗ The Fringe-lipped Bat (*Trachops cirrhosus*) is a carnivorous bat, seen here eating a frog in Panama.

NYCTERIS THEBAICA

Egyptian Slit-faced Bat

Versatile fluffy gleaner

SCIENTIFIC NAME	*Nycteris thebaica*
FAMILY	Nycteridae
DIET	Various arthropods, including katydids, beetles, and spiders
HABITAT	Wide habitat tolerance
CONSERVATION STATUS	Least Concern
WEIGHT	0.21–0.42 oz (6–12 g)
WINGSPAN	11.1 in (28.3 cm)

Slit-faced bats are named for the unusual long slit or cleft that runs down the center of their face, dividing their fleshy nose leaf into a left and right half. Their tails end in a T-shape, formed from cartilage.

The Egyptian Slit-faced Bat, like its fellow *Nycteris*, has long and shaggy fur, tiny eyes, elongated ears, and short, broad wings that provide remarkable maneuverability in tight, cluttered spaces. This maneuverability allows them to fly close to the ground in cluttered environments, following narrow paths through the vegetation and gleaning their prey from low foliage or the ground.

This species is widely distributed throughout most of sub-Saharan Africa, where it is common. Small, isolated populations occur in Morocco, Saudi Arabia, and Yemen.

The Egyptian Slit-faced Bat is largely found in savannas, but displays wide habitat tolerance, inhabiting nearly all terrains but tropical rainforest and montane areas. They also display versatility in their diets and have been documented to eat multiple types of arthropods, including orthopterans (such as katydids and crickets), cockroaches, moths, beetles, bugs, and spiders. Seasonal differences in their diet reflect food availability, and the flexibility of their eating habits explains their ability to live in many different habitat types.

The Egyptian Slit-faced Bat's pelage varies from pale gray to reddish-brown, with a paler front, to bright orange. Their fluffy fur and large wings and ears make them look larger than they are. In fact, they are among the smallest of the slit-faced bats and are sometimes eaten by Large Slit-faced Bats (*Nycteris grandis*), which are four times their size.

→ With its large ears, the Egyptian Slit-faced Bat is able to clearly hear prey-generated sounds and the soft echoes that return from its quiet echolocation calls.

ANTROZOUS PALLIDUS

Pallid Bat

Jack of all trades

SCIENTIFIC NAME	*Antrozous pallidus*
FAMILY	Vespertilionidae
DIET	Highly variable, mostly arthropods
HABITAT	Arid and semiarid regions
CONSERVATION STATUS	Least Concern
WEIGHT	0.49–1.0 oz (14–29 g)
WINGSPAN	5–16 in (37–41 cm)

Pallid Bats are easily identified by the white fur on their front and yellowish-brown to cream fur on their backs. Another distinguishing feature are large ears, which are nearly half as long as the total length of their head and body.

Like other vespertilionid bats, the Pallid Bat has a relatively simple muzzle without a nose leaf. However, wart-like bumps (pararhinal glands), associated with hair follicles, are distributed across the face and are responsible for their musky odor. Inhabiting arid and semiarid environments, Pallid Bats have adapted to low water availability by producing highly concentrated urine.

The Pallid Bat, a gleaner, has a diversified diet. In addition to scorpions, crickets, and spiders, it occasionally feeds on nectar—the only bat in the large Vespertilionidae family that does so. Lacking the long snout or brush-tipped tongue of specialized nectar feeders, it plunges its head and upper body into the flower while holding the flower rim with its wings and feet. For 6 to 8 weeks each year, nectar may provide a predictable and plentiful source of energy. Rounding out its expansive palate, the Pallid Bat has also been documented to capture lizards and small rodents.

This species is very sensitive to human disturbance and may readily abandon a roost. In general, Pallid Bats have a higher predation risk than other bat species because they capture prey on the ground, which may explain their skittish nature. Colonies range from 20 to 200 individuals and female Pallid Bats give birth within maternity colonies in May and June. Older females give birth to one set of twins each year whereas yearling females only have a single pup.

→ The Pallid Bat is distinct enough from its vespertilionid relatives that it is placed in its own genus. With only one species, the genus *Antrozous* is considered monotypic.

LEPTONYCTERIS YERBABUENAE

Lesser Long-nosed Bat

Tequila bat

SCIENTIFIC NAME	*Leptonycteris yerbabuenae*
FAMILY	Phyllostomidae
DIET	Nectar, pollen, and soft fruits
HABITAT	Deserts and dry tropical forests
CONSERVATION STATUS	Near Threatened
WEIGHT	0.53–1.0 oz (15–28 g)
WINGSPAN	Around 10 in (25 cm)

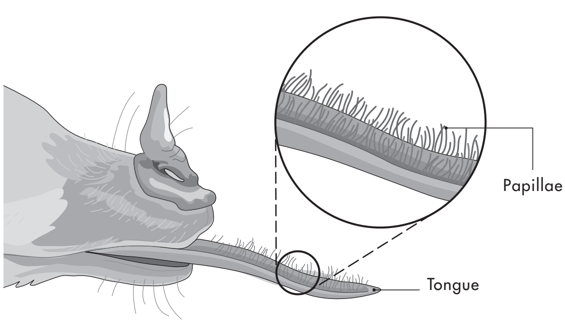
Lesser Long-nosed Bats must visit cactus flowers at least 80 times per night to meet their energy needs. Reaching nectar is facilitated by their long rostrum and long tongues, which mop up the sugary solution with elongated papillae.

Lesser Long-nosed Bats are medium-sized with a small nose leaf and grayish-brown to cinnamon-colored fur. Their lower lip has a distinctive V-shaped groove that serves as a channel for the tongue as it moves rapidly in and out of the mouth bringing in nectar. In the process of obtaining nectar, the Lesser Long-nosed Bat's fur becomes coated with pollen, which it distributes to other plants, including the tequila agave, for which it is a primary pollinator. Bats typically forage alone and may chase other bats away from a flowering cactus.

Roosting in caves and mines in colonies of several thousand bats, this species can be found in thorn scrub and deciduous forest from Arizona to Mexico and into Central America and also in the Sonoran Desert. Because they get all of the moisture they need through feeding, Lesser Long-nosed Bats do not drink and are thus free to roost in areas without water sources. Like many bats, this species faces significant threats from habitat destruction and degradation and from the disturbance and vandalism that sometimes occurs at roost sites. Using one of two well-known migration routes, northern populations of Lesser Long-nosed Bats fly south in the fall and return in spring or summer. In the southern parts of its range bats may be non-migratory.

Tongue with brush-tip papillae

Tiny papillae or extensions on the surface of their tongues increase the amount of nectar that can be carried by the tongue, thus increasing the speed at which a Long-nosed Bat can extract nectar from a flower.



→ Lesser Long-nosed Bats are important pollinators of agave flowers and can hover over them while feeding.

PTEROPUS CONSPICILLATUS

Spectacled Flying Fox

Four-eyed beauty

SCIENTIFIC NAME	*Pteropus conspicillatus*
FAMILY	Pteropodidae
DIET	Fruit, nectar, and pollen
HABITAT	Coastal forests and urban areas
CONSERVATION STATUS	Endangered
WEIGHT	18–36 oz (0.5–1.0 kg)
WINGSPAN	Not known

This strikingly beautiful bat is named for the arrangement of its wing (*ptero* means "wing" and *pus* means "foot"), which starts on the foot rather than the ankle, and for its facial markings (*conspicillatus* means "watching").

Originally described from Queensland, Australia, most of the Spectacled Flying Fox's range is in coastal Papua New Guinea and Indonesia. It is a significant part of the biodiversity of the Wet Tropics World Heritage Area. One of the larger flying foxes, its otherwise black pelage is disrupted by straw-colored rings of fur around its eyes and similar coloring around its neck and shoulders.

Like many flying foxes, it faces significant risks from exploitation, deforestation, habitat degradation, and extreme heat waves. In the Australian population alone, population size has significantly declined, from approximately 250,000 in 2004 to less than 40,000 today. Estimates from the rest of its range are not available, but hunting pressures are significant. As habitat is decreasing throughout its range, it appears to be increasingly using urban sites, including parks and orchards.

The Spectacled Flying Fox primarily consumes nectar and pollen from plants in the Myrtaceae (the myrtle family) and fruit from the Moraceae, a family that includes figs. Data from telemetry studies (in which bat movement is tracked by an attached radio or GPS logger) indicate that bats can fly up to 30 miles (50 km) from their roost site (or camp) nightly in search of food. This highly mobile species changes campsite frequently, even weekly for some individuals. Reproduction is highly seasonal. In the Australian range, mating occurs between March and May and females give birth to a single pup between October and December, just before the heaviest rains of the year. After weaning but before they are fully independent, young bats hang out together in nursery trees within the camp.

→ The handsome Spectacled Flying Fox can use its large wings to shade itself from the sun, and also to fan its body in order to cool off during summer heat waves.

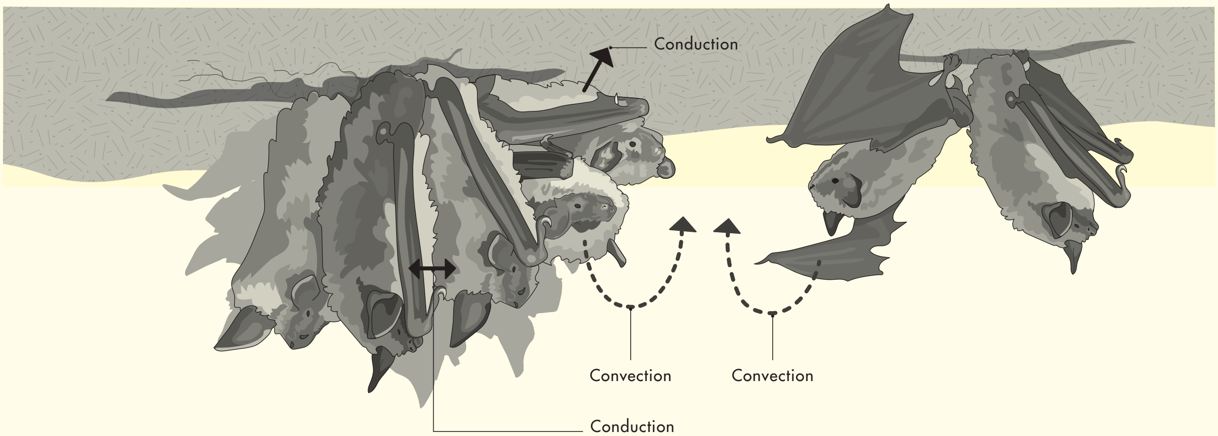
THERMOREGULATION

Understanding thermoregulation

Bats exploit nearly all biogeographical spaces not only as a result of their expansion into multiple dietary niches, but also because they are masters of maintaining energy balance. Deploying the powers of both endothermy and heterothermy allows them to thrive across multiple habitat types from the Arctic to the deserts to the tropics.

To understand thermoregulation in bats one must start with understanding how animals gain and lose heat to and from the environment as well as when and how they choose to maintain body temperature within specific ranges. Heat transfers between the environment and an animal through four processes: radiation, conduction, evaporation, and convection.

Radiation is the transfer of heat through the air in the form of electromagnetic waves, such as the warmth radiated from an open fire or the sun, which is absorbed by animals. Conduction is the transfer of heat through direct contact between objects or substances and an animal, such as the loss of heat from a bat roosting on a cold cave wall. Evaporation involves the conversion of a liquid such as sweat on a warm body surface into a vapor. As sweat, saliva, or another fluid evaporates from the surface of the skin or respiratory tract, it takes away heat from the body. For bats such as the Lesser Mouse-tailed Bat (*Rhinopoma hardwickii*, page 178) that roost in environments that are hotter than their core body temperature, evaporative cooling is a primary mechanism by which they can cool down (even though it poses a dehydration risk). Finally, convection, for terrestrial animals, is the transfer of heat through the movement of air. As air next to an animal's body is heated through radiation, it becomes less dense and rises (dissipating heat), then is replaced by cooler air. The effects of convection are enhanced by wind,



Conduction and convection in bats

Roosting bats can gain or lose heat by conduction. For example, bats in a cold cave will lose body heat when in contact with the cold cave wall and can also lose heat to a bat that is clustered, or physically in contact with it. Bats can also lose heat through convection, when their body is warmer than the surrounding air. Convection from outstretched wings, with their two-sided surface, is greater than convection from furred areas of the body.

← Bats in temperate climates, like the Brown Long-eared Bat, can save energy by hibernating in the winter. Note the frozen condensation in its fur.

→ Even in the tropics, bats like this Gambian Epauletted Fruit Bat may drop their body temperature to save energy.

cooling down an animal even faster. Flying bats may transfer the excess heat generated during flight to the environment through both radiation and convection.

CRUCIAL FOR SURVIVAL

The maintenance of body temperature, or thermoregulation, in the face of ever-changing temperatures and humidity is critical to survival. Different animals employ different strategies depending on their physiology, habitat, the prevailing environmental conditions, and their evolutionary history. Animals, like most mammals and birds,

that have the capacity to generate their own body heat are endothermic, whereas those that rely on external heat sources are ectothermic. These are the more precise scientific terms for what are colloquially and somewhat incorrectly called "warm-blooded" and "cold-blooded." Independently of how they warm their bodies, animals can also be categorized as homeothermic if they maintain a constant body temperature or heterothermic if their body temperature fluctuates.

Most mammals, like birds, are endothermic homeotherms. This means they can generate their own body heat by increasing their metabolic rate and maintain their core body temperature within a small range called the set zone. Core body temperature is controlled by the hypothalamus in the brain, which acts like a master thermostat.

TEMPERATURE LIMITS

The range of environmental temperatures within which an endothermic animal can maintain its normal body temperature without having to expend extra energy for thermoregulation is called the thermal neutral zone (TNZ). In the TNZ, the metabolic rate of an animal, typically measured by the rate of oxygen consumption, is at its lowest and the physiological mechanisms for heat production or heat loss are minimally deployed. When the ambient temperature rises above an animal's upper critical temperature (UCT), animals must deploy mechanisms to cool down. These mechanisms can be physiological, behavioral, or anatomical. There is little leeway above the UCT and animals risk heatstroke and death above this range. For example, in the unprecedented heat wave of the Australian summer of 2019–2020, tens of thousands of Gray-headed Flying

Foxes (*Pteropus poliocephalus*), including pups, died. Paradoxically, the mechanisms for cooling down, like the fanning of wings and panting, requires increased metabolic activity and leads to dehydration, which further stresses the body.

When the ambient temperature dips below a given animal's lower critical temperature (LCT), most species will increase their metabolic rate and alter other physiological processes and behavior to maintain their preferred temperature. Although all bats are endothermic and can generate their own heat, many species are heterothermic and allow their body temperature to vary, most commonly by using torpor: decreasing metabolic rate and temperature in cold environments. Torpor allows for significant energy savings and can be deployed for minutes, hours, or days as needed.

↖ One way to cool down is to get wet. Most bats cannot swim well but a quick splash in water helps this Gray-headed Flying Fox cool down.

↑ Above their upper critical temperature, these Gray-headed Flying Foxes can no longer regulate their body temperature and may die from extreme heat.

Bat thermodynamics

Bats are typically included in the "small mammals" category, which also contains rodents and shrews. Being a small mammal poses specific physiological challenges that typically result in fast-paced life histories and relatively short lives. However, bats, with their unique physiology and the large surface area of their wings, handle these challenges differently and live much longer.

Small mammals have higher energy needs per ounce of body mass than larger mammals. This difference is due to simple geometry and biology, which can be understood best by considering a hypothetical ball-shaped animal. Inside the ball are all the body organs and tissues, the body core, in which metabolic activity occurs. The heat required by an endotherm is generated in this three-dimensional core, proportional to the volume of the animal. The surface of the ball is the animal's skin, from which heat is lost. The surface is two-dimensional and could be laid out on a flat surface.

Biologists calculate the surface-area-to-volume ratio as a way of considering how heat is generated and lost in animals of various sizes. As you can see, even though small, ball-shaped animals and large, ball-shaped animals have the same shape, the smaller animals have a higher surface-area-to-volume ratio.

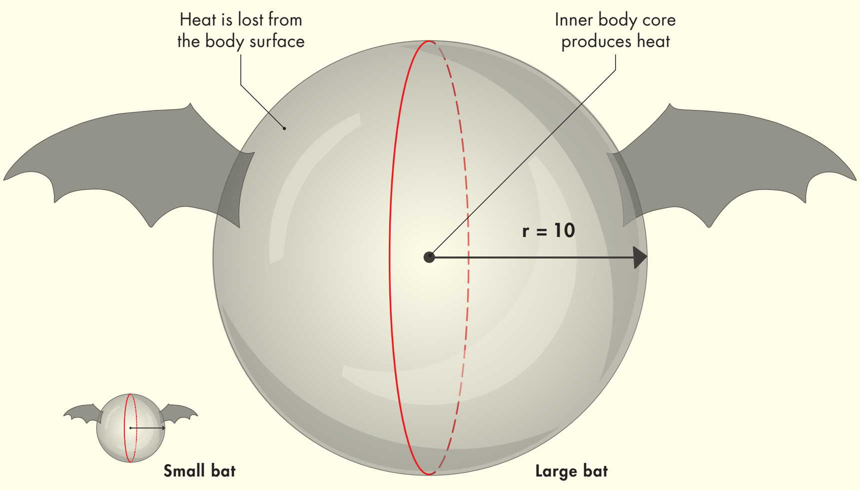
Being smaller and having a high surface-area-to-volume ratio has well-studied physiological consequences. Smaller animals lose heat at greater rates compared to larger animals of the same shape, and thus require greater energy just to survive. This is true even

Body core heat in bats

Body heat is generated inside a bat's body and can be lost to the environment across the surface of a bat's skin. Geometry shows us how smaller bats have a greater surface-area-to-volume ratio than larger bats; they lose heat more readily and must consume more calories to meet their energy needs than larger bats.

Small bat (radius = 1 in)
Surface area = 12.6 in^2
Volume = 4.2 in^3
Surface area/volume ratio = 3.0

Large bat (radius = 10 in)
Surface area = 1,260 in^2
Volume = 4,200 in^3
Surface area/volume ratio = 0.3



within one animal lineage like bats, in which the largest flying foxes are up to 750 times bigger than the smallest insect-eating bats. Relatively smaller endothermic mammals, like bats and rodents, have higher mass-specific basal metabolic rates than larger mammals, such as dogs, hooved mammals, and the like. Relative to larger mammals, their thermal neutral zone (TNZ) is narrower and their lower critical temperature (LCT) is much higher. Smaller mammals like bats have trouble staying warm in cold environments and as a result may choose to be heterothermic, deploying torpor to save energy.

DEALING WITH HEAT AND COLD

Although the ball-shaped animal analogy helps us understand the math behind size differences in thermoregulation, it has its limits. For bats, there are two additional thermoregulatory considerations. The first is that their large wing membranes dramatically increase the total skin surface area and thus the surface-area-to-mass ratio. The wings of one of the largest bat species, the Golden-capped Flying Fox (*Acerodon jubatus*), for example, are relatively broad and span more than 5 ft (1.5 m). The second is that bat flight, powered by increased metabolic rates, is very energetically expensive and elevates body temperature. Most bats need to dissipate this heat so as to prevent significant hyperthermia during flight.

↑ The large surface area of the Golden-capped Flying Fox's wings allows it to rapidly dissipate the excess heat that is produced when flying.

Bats can dissipate heat from both the back and the front side of their wings, aided by convection. Unlike bird wings with their feathers, the bat wing is largely naked and thus uninsulated. As such, it serves as a "thermal window," a surface across which heat is readily dissipated. These effects are enhanced by the presence of blood vessels in the wing, which can be extensive. When these vessels dilate, more blood, and thus heat, is brought to the surface where it can dissipate, cooling the body. Bats can deploy this strategy to purposefully dissipate heat either when flying or when roosting. To conserve heat, bats can constrict these vessels, keeping more of their warm blood in the body core. Bats can also decrease the degree to which their wings are exposed to the air and thus decrease heat loss by wrapping them tightly around themselves or by tightly clustering with other bats.

→ Bats can shield themselves from the sun and minimize heat loss by wrapping their wings tightly around themselves, like this Little Red Flying Fox.

↙ Brandt's Myotis is native to Europe and Western Asia, where it feeds along waterways and in woodlands.

HOW BATS BREAK THE RULES

Non-flying small mammals generally display "fast" life histories. Tied to their higher metabolic rates and ecological factors such as high predation rates, species with fast life histories invest a significant proportion of their energy in reproduction rather than long-term survival. Rodents, as classic examples of small mammals with fast life histories, reproduce at an early age, produce numerous offspring in a short period, and have a shorter life span.

Bats, with their unusual physiology, break these life history rules spectacularly. Despite their relatively small size, they have low reproductive rates, with most bats producing a single pup once a year, and they live exceptionally long lives. The oldest known free-ranging bat was a male Brandt's Myotis (*Myotis brandtii*), which lived at least 41 years. Multiple other species live more than 25 years in the wild, including the Greater Horseshoe Bat (page 176) at 30.5 years and the Gray Long-eared Bat at 25.5 years. Scientists are still uncovering their secrets, but it appears that the molecular mechanisms that have evolved to combat the cellular damage caused by high body temperatures during extended flights may be the key to bats' long lives, and also their uniquely low levels of cancer and efficient immune responses.

How bats save energy

Since powered flight requires so much energy, bats must maximize energy gain but also minimize energy loss. Excess energy gained from food can be converted to fat for use in leaner times. Bats manage their energy stores through roost selection and regional and whole-body heterothermy.

Recorded weights for a given bat species often vary significantly due to a bat's current feeding status, its sex, reproductive state, and overall body condition. The lowest weights are typically recorded in nonpregnant bats that have just emerged from their roost at around dusk. These pre-prandial bats are breaking their fast and may also be dehydrated. After finding a drink, most species will then feed for several hours before resting. They may return to their day roost at this time or, like the Lesser Horseshoe Bat (*Rhinolophus hipposideros*) in the United Kingdom, may rest in a night roost closer to their foraging site, feeding again just before dawn.

← Lesser Horseshoe Bats sometimes roost in human-made structures. After feeding at dusk they may rest in a different roost than the one they occupy during the day.

↗ Townsend's Big-eared Bat is a champion eater, packing on the ounces in preparation for the long winter.

Postprandial bats can weigh 50 percent or more than they did at the nightly emergence, depending on feeding success and diet. Bats may store excess energy at certain times of the year in the form of white adipose tissue and/or brown adipose tissue, which can later be used to produce energy and heat, respectively.

Townsend's Big-eared Bats (*Corynorhinus townsendii*, page 172) provide a good example of weight fluctuation, as their weight naturally varies between 0.17 and 0.46 oz (5 and 13 g). In the late fall, over a span of seven weeks, females of this temperate hibernating species gain 32 percent of their body mass in the form of fat. Such marathon feeding favors overwinter survival and reproductive success the following year. Under normal circumstances, leptin, a hormone produced by fat and circulating through the bloodstream, provides body condition information to the mammal brain. As fat increases, so do leptin levels, letting an animal know that it can rein in its appetite. Bats, however, ignore this hunger-regulating hormone signal in order to keep eating despite already being rotund.

ROOSTING BEHAVIOR

In addition to altering their feeding behavior, bats manage energy balance with changes in roosting behavior. Bats select their roosts largely on the basis of the microclimate found within and may choose different roosts at different times. For example, pregnant bats and those nursing young roost in places that are warm, which allows for energy savings. Bats that roost in large, tightly clustered groups like the Indiana Myotis both reduce their exposed surface area and gain the insulative benefits of heat conduction from their neighbors. For very large, non-hibernating cave colonies, like the Wrinkle-lipped Free-tailed Bat (*Mops plicatus*), the sheer number of bats in a cave can collectively generate enough body heat to raise the temperature in the dome of the cave, which facilitates the rapid growth of bat young. Cold roosts, such as attics and temperate zone caves, are used by bats that hibernate and save energy by allowing their body temperature to drop close to ambient.

↑ Some bat species conserve energy by roosting in very large, densely packed clusters, like Schreibers's Long-fingered Bat from Eastern Europe.

→ Mouse-eared Myotis (*Myotis myotis*) are saving energy by clustering together in a hole in the roof of an abandoned railway tunnel in Bosnia and Herzegovina.

THERMOCONFORMING

Bats are masters at saving energy through thermoconforming, and at different times across different species around the world, they will utilize the full spectrum of heterothermic possibilities, from regional heterothermy to daily torpor to hibernation. The typical presentation of regional heterothermy is the dropping of temperature at the periphery of the bat's body while protecting the temperature of the furred body core.

Advances in technology, such as the use of tiny temperature-sensitive data loggers attached to bat backs and thermocouple probes inserted into flight muscles, have revolutionized our understanding of bat thermal biology. Likewise the use of thermal infrared cameras that can view temperature differences by body region has unlocked the secretes of regional heterothermy. In fact, thermal camera images led to the discovery of vascular "radiators" on the sides of Brazilian Free-tailed Bats. Exceptionally warm spots on each side of the bat's abdomen corresponded to a hairless patch of skin in which a highly organized network of blood vessels was found. These thermal windows facilitate the rapid dumping of heat during flight, as these bats may travel up to 35 miles (56 km) in a single feeding bout and are often under significant heat stress.

Researchers examined museum specimens of dozens of other free-tailed bats (those in the family Molossidae) and noted the same vascularized thermal window. This includes Pallas's Mastiff Bat (*Molossus molossus*) from Martinique in the Lesser Antilles, the first free-tailed bat to be scientifically described, in 1766. This anatomical marvel, clearly visible to the naked eye, was simply not noted before a thermal camera revealed its secrets.

Daily torpor

While roosting, many bats will take advantage of cooler temperatures when they find them. Depressing metabolic activities and thermoconforming, or going torpid, for hours or even just a handful of minutes each day can save precious energy reserves.

With few exceptions, bat bodies are well covered with fur. The nearly hairless Greater Naked Bat (*Cheiromeles torquatus*, page 170) is an anomaly as a relatively large bat surviving in a warm environment. The bat fur coat, however, is an insufficient insulator and most bats, even in the tropics, will deploy torpor in a variety of circumstances. The ability to "turn off" or depress metabolic activity and thus passively cool one's body when ambient temperature is low saves energy for later use. It can also help mitigate the costs of unsuccessful foraging due to unpredictable food availability or poor weather. Using torpor also reserves precious energy for expensive activities like pregnancy, lactation, migration, and fighting infection.

Bats will actively seek out locations with the most favorable temperatures for energy savings, selecting roost sites with advantageous microclimates. Torpor has now been documented in nearly every bat family across nearly every habitat type, suggesting that heterothermy is an ancient bat trait and thus likely a significant contributor to the evolutionary success of bats. Daily torpor can take a variety of forms, from a single bout to multiple shorter bouts per day, sometimes called "micro" torpor bouts.

Torpor has generally been associated with cold temperatures, but we now understand that its expression is diverse and malleable. For desert bats, like the Lesser Mouse-tailed Bat, temperatures can fluctuate widely and dehydration is a significant risk in the dry heat. Bats exposed to very high temperatures may deploy "hot torpor," in which metabolic activity is minimized, thus saving water, and the body allowed to thermoconform, in this case to get warmer. This allows bats to increase their heat tolerance, but is high risk as they have few mechanisms to cool down if the ambient temperature rises above a critical threshold.

← The Californian Leaf-nosed Bat (*Macrotus californicus*) survives in the desert by selecting cool roost sites in the summer.

→ The bodies of nearly all bats have a fur coat that provides insulation against the cold, like this Bornean Horseshoe Bat (*Rhinolophus borneensis*).

Hibernation

Hibernation is the use of torpor over multiple days. It can last for weeks or months. It is especially common in overwintering insectivorous bats that live in cold, inhospitable habitats with little available food, but is also displayed in some subtropical and tropical bats.

An extension of daily torpor, hibernation is the prolonged, multiple-day depression of metabolic activity to conserve energy, especially when food is not available. For insect-eating bats, like the Greater Horseshoe Bat and the Tricolored Bat (*Perimyotis subflavus*), availability of this seasonally plentiful food source becomes negligible in temperate zone winters because insects, as ectotherms, fare poorly in the cold and time their own life cycles to the warmer summer months. To prepare for this lean, cold period, bats increase eating in the late summer and fall.

Hibernating bats must then select an appropriate site in which to wait out the longer winter; this is often caves but also sometimes tree hollows. Some bat species are also perfectly happy to hibernate in human-made structures such as attics and abandoned mines. The hibernating Ussurian Tube-nosed Bat (*Murina ussuriensis*) is unusual in that it hibernates under the snow. At least in the species studied to date, bats typically return to the same winter roosts each year.

Winter roosts used for hibernation vary significantly from those used in the active season in that they have cold, stable temperatures. Each bat species appears to have its own hibernation microclimate preferences in terms of temperature and humidity, and bats display species-specific hibernation patterns. These include the overall length of hibernation, the number of days spent in each bout of torpor, and the lowest temperature that they display in torpor.

Some species enter hibernation earlier in the fall and emerge from hibernation later in the spring than others. Even within a species, such as the Little Brown Myotis, this varies geographically, with the longest hibernation displayed in its northern Canadian locations. Daily torpor and the torpor of hibernation can be described as either shallow, in which metabolic processes are only reduced by approximately 10–15 percent, or deep, in which metabolism may decrease by 99 percent. The heart rate of the Little Brown Myotis during hibernation may slow to 20 beats per minute or lower; quite a change from the 1,000 beats per minute they exhibit while flying!

BRIEF AROUSALS

Hibernation patterns and their underlying physiology have been well studied in a handful of model bat species, including the Mouse-eared Myotis and the Greater Horseshoe Bat. In this species, similar to what has been found in other bats, those bats that roost at the coldest temperatures (and are thus able to save the most energy) display the longest torpor bouts—lasting 12 days or more. Like all mammal hibernators, from bears to lemurs to dormice, torpor bouts in bats are interrupted by arousals to "normal" temperatures. The functions of these arousals, which are relatively short in bats, lasting 60–90 minutes, are not completely understood, but evidence suggests that they are important for regulating water and electrolyte balance, sleep (which does not occur in deep torpor), and

← Hibernating Tricolored Bats will arouse periodically over the winter months, perhaps to mate or find a drink of water.

↗ The Ussurian Tube-nosed Bat is the only mammal besides the Polar Bear (*Ursus maritimus*) to hibernate in the snow.

→ Temperature-sensitive dataloggers attached to bats, like these Little Brown Myotis, can record their thermoregulatory behavior during hibernation.

immune function. Some bats may even mate during these brief periods. In mild conditions, where bats are roosting near cave entrances, the bats may time these arousals to dusk and attempt to forage. A bat that arouses within a tight cluster of other bats may trigger arousals in its neighbors.

Although arousal bouts are clearly advantageous and serve to "reboot" physiological processes after metabolic depression, arousal in cold environments expends significant energetic resources. In Little Brown Myotis, each arousal burns about 108 mg of the approximately 1,800 mg of stored fat. These arousals are largely fueled by brown adipose tissue, which contains a high number of mitochondria—the cell's energy factories. The presence of densely packed mitochondria gives brown adipose tissue its distinctive coloration; differences in proteins expressed in its cells result in the release of energy in the form of heat rather than adenosine triphosphate (ATP), which is the energy currency of all other cells. Bats that enter hibernation with low fat reserves, a frequent occurrence in young of the year, or that are disturbed by humans during hibernation may not survive the winter.

Some bats, such as the Hoary Bat (*Lasiurus cinereus*, page 174) from North America, avoid the challenges of hibernation by adopting a different strategy. Each fall, hundreds of Hoary Bats from the United States migrate to the warmer climate of northern Mexico.

→ Greater Horseshoe Bats roost in large numbers when hibernating, but are not clustered tightly together.

CHEIROMELES TORQUATUS

Greater Naked Bat

Weird and wonderful

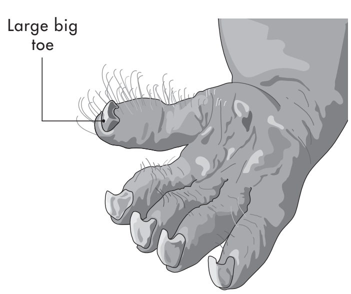
SCIENTIFIC NAME	*Cheiromeles torquatus*
FAMILY	Molossidae
DIET	Beetles
HABITAT	Tropical lowlands and marshes
CONSERVATION STATUS	Least Concern
WEIGHT	5.3–6.9 oz (150–196 g)
WINGSPAN	25 in (63.5 cm)

The Greater Naked Bat is the heaviest hawking insectivorous bat (one that catches prey on the wing). It is a fast flier that forages in open areas.

Greater Naked Bats, with their black or blackish-gray skin, are not completely hairless; rather their body is covered in very short, sparse hairs. A reduction in fur translates to less drag and thus improved aerodynamics. Due to their relative size, they lose heat to the environment less readily than smaller bats. As they live in tropical Southeast Asia, the insulative properties of fur are less important.

Enlarged big toe

The large and opposable big toe has bristle-like hairs that aid movement when on the ground.



Greater Naked Bats are formidable, both in the air and on the ground. Like other free-tailed molossid bats, their wings are tougher and contain more muscles than other bats, allowing them greater control over the shape of the airfoil. Given the reduction in size of the uropatagium, molossids catch food directly in their mouths rather than using their feet and tail membrane to scoop up prey. The hind limbs of the Greater Naked Bat are especially muscular and stocky—this bat can move quickly on the ground or along a rock face when needed. This cursorial movement is aided by the reduced uropatagium, pouches on the side of the body into which the wing membranes can be tucked out of the way, and an opposable first toe with short, bristle-like hairs for better grip.

Both male and female Greater Naked Bats have a fold of skin at the neck called the gular sac or pouch which contains glands. The glands are surrounded by long hairs and secrete a smelly, oily, and viscous substance, likened to "stale socks drenched in engine oil."

→ The scientific name for the Greater Naked Bat, *cheiro* plus *meles*, means hand plus limb, in reference to its hand-like foot.

CORYNORHINUS TOWNSENDII

Townsend's Big-eared Bat

Ear curler

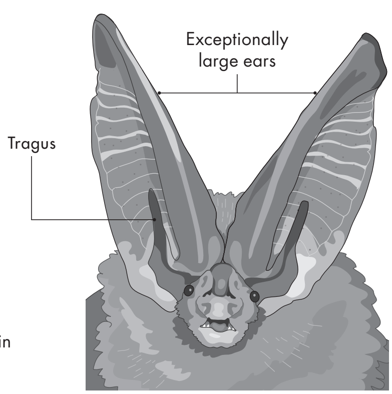
SCIENTIFIC NAME	*Corynorhinus townsendii*
FAMILY	Vespertilionidae
DIET	Moths and other small insects
HABITAT	Variable, including forests, and arid and semiarid habitats
CONSERVATION STATUS	Least Concern, except for the subspecies *C. townsendii ingens* and *C. townsendii virginianus*
WEIGHT	0.18–0.46 oz (5–13 g)
WINGSPAN	Around 11 in (28 cm)

Townsend's Big-eared Bat is a relatively small species in which females are slightly larger and heavier than males. Its most remarkable feature is large ears, which are over 1.4 in (3.5 cm) long and connected by a low band across the forehead.

The fur of Townsend's Big-eared Bats is long and bicolored, with blackish bases and tips that vary between yellowish and cinnamon-brown to slate-gray on their back and buff or pale brown on their front. There are two large glands on either side of the muzzle. The face, ears, and wing membranes are grayish-brown.

Within the broadly distributed North American Townsend's Big-eared Bat, five subspecies are recognized. Two of these, the Ozark Big-eared Bat (*C. townsendii ingens*) and the Virginia Big-eared Bat (*C. townsendii virginianus*), each isolated in specific regions of the eastern United States, are Endangered, whereas the remaining subspecies are stable. Endangerment is tied to these bats' very specific roosting requirements and few hibernacula. For example, the Ozark Big-eared Bat is only found in cave and karst areas surrounded by undisturbed oak-hickory hardwood forests. Since Big-eared Bats have strong roost fidelity, meaning that they return to the same maternity sites and hibernacula each year, human disturbance of roost sites and loss of critical forest habitat pose significant threats.

Like other hibernating vespertilionid bats, Townsend's Big-eared Bats prepare for hibernation with significant weight gain. Once settled in the hibernaculum, bats of this species avoid heat loss across their enormous ears by curling them back over the head. Thankfully, the fungal pathogen that causes the bat disease White-nose Syndrome in hibernation does not affect this species.



Large ears
Note the large ears that join in the middle and the very long tragus within the ear.

→ Townsend's Big-eared Bat is a common species found in the caves of western North America.

LASIURUS CINEREUS

Hoary Bat

Silver-tipped beauty

SCIENTIFIC NAME	*Lasiurus cinereus*
FAMILY	Vespertilionidae
DIET	Moths and various other insects
HABITAT	Forests
CONSERVATION STATUS	Least Concern
WEIGHT	0.71–1.23 oz (20–35 g)
WINGSPAN	13–16 in (34–41 cm)

The Hoary Bat is common and widely distributed throughout the Americas; populations reported from the islands of Hawaii are now recognized as a separate species (*Lasiurus semotus*), as are Hairy Hoary Bats from South America (*L. villosissimus*).

The Hoary Bat roosts solitarily in deciduous or coniferous tree foliage, 10–60 ft (3–20 m) above the ground. Hanging in the open from a branch or twig, the Hoary Bat prefers trees that are larger than average in diameter, taller than average, and in stands dominated by mature trees. Their distinctive salt-and-pepper coloration and furred tail membrane help camouflage them from below. They are easy to identify when flying, however, by their larger size and swift, erratic flight. Mating occurs during the fall, but implantation of the developing embryo into the uterus is delayed until spring, with pups born in early summer. Females typically have twins, but litters of 1 to 4 pups have been documented.

Many Hoary Bats, when faced with the oncoming winter, choose not to save energy by thermoconforming and hibernating below ground. Rather, they migrate south to warmer climates. The Hoary Bat's migration patterns and other aspects of its biology are relatively well studied in North America, but the picture is far from complete and some individuals may, in fact, hibernate. During migration Hoary Bats are often observed in the daytime, but otherwise this species emerges late in the evening, well past sundown. Due to its migratory behavior, the Hoary Bat is one of the most common species killed at wind-energy facilities. An estimated 76,000 to 152,000 Hoary Bats are believed to be killed each year by collisions with wind turbine blades, presenting a conservation challenge for this otherwise common species.

→ The Hoary bat is readily identified by its ragged, salt-and-pepper frosted fur and yellowish throat.

RHINOLOPHUS FERRUMEQUINUM

Greater Horseshoe Bat

Largest European horseshoe bat

SCIENTIFIC NAME	*Rhinolophus ferrumequinum*
FAMILY	Rhinolophidae
DIET	Highly variable, including myriad arthropods (especially moths)
HABITAT	Highly variable, but mostly forests
CONSERVATION STATUS	Least Concern
WEIGHT	0.46–1.55 oz (13–44 g)
WINGSPAN	13.8–15.7 in (35–40 cm)

Broad wings and a well-developed uropatagium endow the Greater Horseshoe Bat with highly maneuverable, fluttering flight and the ability to hover. Young bats begin practicing their flight skills 15 days after birth and are proficient fliers at 24 days old.

The Greater Horseshoe Bat is a versatile hunter and adapts its diet according to food availability. It can catch prey by slow aerial hawking (in flight), ground gleaning (for non-flying prey), and by fly-catching from perches. In this instance, bats emit search echolocation calls from a perch; when an insect is detected, the bat flies a short distance to retrieve it and returns to the perch to consume it.

The Greater Horseshoe Bat is widely distributed across the Palaearctic, occurring from North Africa and southern Europe through Southwest Asia, the Caucasus, Iran, Afghanistan, Pakistan, and the Himalayas. After precipitous declines in some parts of Europe, the Greater Horseshoe Bat is uncommon across most parts of its range except in parts of Southwest Asia and the Caucasus, where it is abundant. In its northern distribution, this species hibernates in large caves. Although hibernacula may contain as many as 500 bats, they may roost separately while in torpor rather than clustering tightly as most species do. In hibernating populations, mating occurs in the fall and females store sperm in their reproductive tracts all winter, ovulating and conceiving after the spring emergence from hibernation. Active (non-hibernating) bats across the range roost in multiple locations, including abandoned human-made structures. To the dismay of parishioners, they have a fondness for old church buildings.

→ Greater Horseshoe Bats have a diverse palate and can shift prey sources regionally and seasonally.

RHINOPOMA HARDWICKII

Lesser Mouse-tailed Bat

Semiarid specialist

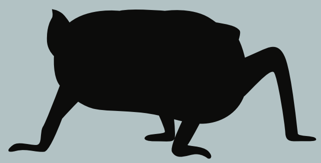
SCIENTIFIC NAME	*Rhinopoma hardwickii*
FAMILY	Rhinopomatidae
DIET	Predominantly flying ants and termites, and beetles
HABITAT	Dry, semiarid environments
CONSERVATION STATUS	Least Concern
WEIGHT	0.23–0.42 oz (6.5–12 g)
WINGSPAN	Around 12 in (30 cm)

The Lesser Mouse-tailed Bat is one of six species in the unique and unusual bat family Rhinopomatidae. Adapted for living in semiarid regions and eating social insects, they have a complex suite of adaptations.

The most noticeable feature of mouse-tailed bats is a long tail that is mostly free of the uropatagium, or tail membrane. It is composed of more tail vertebrae (13 to 16) than all other species of bats (none up to 11). The proportions of the wings of mouse-tailed bats are also unique; for example, the wingtip is extremely short, but the humerus and radius are very long, giving the wing a high aspect ratio and facilitating fast, straight flight. This genus of bats is named for their unusual, valvular, slit-like nostrils which are capable of sealing completely (*Rhino* means "nose" and *poma* means "cover"). Closure of these valves when not actively breathing conserves water in arid environments. Mouse-tailed bats have large eyes relative to other insect eaters, which may reflect a role for optical cues for orientation and navigation.

The Lesser Mouse-tailed Bat survives the dry season by using torpor, fueled by accumulations of white fat in the abdomen and the base of the tail. This fat is acquired in the monsoon season by consuming large amounts of fatty flying ants and termites, which emerge in massive reproductive aggregations. As fat is metabolized to produce energy, water is also released, meeting their water requirements during this lean period. In other periods of the year, the Lesser Mouse-tailed Bat consumes small to medium-sized beetles and occasionally other insects.

→ Mouse-tailed Bats have a number of unique anatomical features, including differences in wing bone structures. The purpose of their very long tails is unknown.



REPRODUCTION

Finding a mate

Like other mammals, monogamy is rare in bats, with most species displaying either polygyny or promiscuity. Regardless of the mating system, males and females, which typically roost separately, must find one another and choose with whom to mate at the appropriate time.

Monogamy is very common in birds but rare in mammals due to differences in the reproductive costs and strategies for males and females in each taxonomic group. Unlike birds, where the costs for males and females are similar and males can help incubate eggs and care for chicks, male mammals have little opportunity to contribute to the care of their offspring, being unable to participate in the energetically expensive pregnancy and lactation undertaken by female mammals. This drives males to pursue a strategy of mating with as many females as possible, which often requires competing with other males and may drive females to be especially choosy about mate selection.

Some bat species, such as the Noctule (*Nyctalus noctula*), display promiscuity, with males and females both seeking multiple mates, while others, like the Florida Bonneted Bat (*Eumops floridanus*), are polygynous, with one or a few males monopolizing access to multiple females. The Yellow-winged Bat (*Lavia frons*, page 210) from sub-Saharan Africa is one of the few bat species documented to be monogamous. Yellow-winged Bats are territorial and live in pairs, roosting within 3 ft (1 m) of each other in the crowns of acacia trees. They take turns watching for predators during the day and males patrol the territorial boundaries each morning and evening. In what is likely courtship behavior, males and females engage in "aerial ballets," swooping and circling around each other.

← The Noctule congregates in large numbers and is sexually promiscuous; both males and females may mate with multiple individuals of the opposite sex.

↑ A single male, or perhaps a very small group of males, controls access to a group of female Florida Bonneted Bats. This species is classified as polygynous.

LEKKING AND CALLING

Perhaps the most interesting mating behavior in bats occurs in those that "lek." Best described in birds, a lek is a gathering of males for the purpose of competitive displays aimed at attracting females. In this system of indirect male-male competition, strong female mate choice is present in which females judge male quality by evaluating their display. In bats, the best-known example is the Hammerhead Bat (*Hypsignathus monstrosus*, page 208), a pteropodid fruit bat from Central and West Africa. Between 20 and 135 males of this species, which are nearly twice the size of females (and the largest bats in Africa, with a wingspan of nearly 3 ft/90 cm), station themselves along branches and attempt to attract females with a ritualized display of wing beating and the emittance of a loud honking sound. This deep, loud sound is produced by vocal cords within a greatly enlarged larynx; sound travels to large resonating chambers that connect to a large sinus in the male's enlarged snout (hence the name derived from the shape of the skull), amplifying their calls.

Males compete for access to the best display locations, claiming an area approximately 33 ft (10 m) in diameter. In the early evening, females fly through the lek and select a male by landing next to him. In response, the male emits a "staccato buzz" call, which

is followed by copulation that lasts less than one minute. Females depart immediately after copulation and males resume their ritualistic display! The efforts of the males pay off for the chosen ones; researchers documented that the top 6 percent of males achieve 79 percent of total matings. With this difference in physical appearance and the significant size difference between males and females, this unique species displays more sexual dimorphism than any other bat species in the world.

Lekking has also recently been described in another bat with an inexplicably strange face, the Wrinkle-faced Central American Bat (*Centurio senex*). During courtship, this species' display includes the donning of a mask, which is present only in males. Beneath the male's chin is a furred skin fold that he pulls up to cover the lower half of his face, an apparently attractive behavior.

↖ A single large male Hammerhead Bat may roost among a group of females, which are approximately half his size.

↗ Male Wrinkle-faced Bats display their beauty by pulling a flap of white skin over the lower half of their faces during courtship.

Relatives of the Hammerhead Bat, the epauletted fruit bats (in the genera *Epomophorus*, *Epomops*, and *Nanonycteris*), also use "calling displays" to attract females, even if they do not display the classical and highly organized lek of Hammerhead Bats. Males of these species, with their loose jowls, make a loud "ping" sound, beating their wings in between calls. Their visual displays are augmented by "epaulettes" on their shoulders, like the patches on an officer's uniform. These tufts of white fur, typically concealed within a pouch, can be inverted and displayed to females to enhance their attractiveness.

PHEROMONE ATTRACTIONS

Rather than relying solely on visual and auditory cues, males of many bat species use pheromones to attract females. Within the family Emballonuridae, the sheath-tailed bats, pheromone-containing pouches (wing sacs) in the propatagium have evolved independently in both the New World and Old World lineages. For example, wing sacs in the Naked-rumped Tomb Bat (*Taphozous nudiventris*, page 212), which are much larger in males than in females, contain volatile secretions that are used to spread the male's scent during courtship.

The Greater Sac-winged Bat from Central and South America engages in a unique behavior called "salting" in which males, in hovering flight, spray breeding females with a combination of urine and bodily secretions, which are transferred to and stored in the wing sacs. This ritualized mating display may be accompanied by courtship songs; the most successful males may be able to monopolize a small harem containing three to five females.

↑ The wing sac on a male Greater Sac-winged Bat contains pheromones and other secretions.

HOME SWEET HOME

Male bats may also attract females by claiming the best territories, in which case females are choosing them for their ability to locate and defend the most desirable roosts. One of the most interesting examples of this occurs in the White-throated Round-eared Bat (*Lophostoma silvicola*), in which males use their incisors and canine teeth to excavate a roost hollow in a hardened arboreal termite nest. These nests then presumably attract a small number of females who give birth inside. In this classic example of resource-defense polygyny, the male has created a roost with favorable and stable temperatures that is easy to defend.

Seasonal breeding patterns

Like other animals, bats time their energetically expensive reproductive activities to coincide with periods of peak resource availability. For some species, this is a flush of new insects in early summer, while for others it may be seasonal variations in plant flowering and fruiting. The timing of bat birth is determined not only by controlling when to ovulate and when to mate, but also by delaying fertilization after mating by weeks to months.

As a result of their slow life histories, most female bats are monestrous, reproducing just once per year. Birth of their single (or, rarely, twin) pups is timed to match peak food availability, which varies by species, diet, and habitat type. Many temperate bats, which cope with a lack of food availability and cold winter temperatures by hibernating, have solved the puzzle of how and when to allocate energy to survival and reproduction in a highly unusual manner. They display a dissociated pattern of reproduction (also seen in some snakes), in which the production of eggs and sperm, under

→ Some bat species, like Natterer's Myotis (*Myotis nattereri*), gather outside of caves in the late autumn in advance of a period of pre-hibernating promiscuous mating.

hormonal control, occur at a different time than mating. Each year in the fall, bats like the Northern Myotis (*Myotis septentrionalis*) in North America and the Common Serotine (*Cnephaeus serotinus*) in Europe that display this pattern arrive at hibernation sites and engage in "swarming" behavior. This conspicuous behavior, in which hundreds or even thousands of bats swarm at the mouth of a cave each evening, facilitates promiscuous mating and significant gene flow between bats from different summer roosts.

After mating, often with more than one male, the most amazing thing happens. Once thought to only occur in bats, but now documented in a dozen or so other animal groups, females store and likely nourish sperm within the oviduct and the uterus throughout the winter. In some hibernating species, such as the Little Japanese Horseshoe Bat (*Rhinolophus cornutus*), mating also occurs during the winter when males arouse from torpor and mate with females, who may remain torpid (and thus oblivious as to what has transpired).

Engaging in mating behavior and storing sperm over the winter saves bats precious time in the spring and summer, which may be short-lived in the most northern climates. Upon arousing from hibernation in late spring, females ovulate and the egg is fertilized with one of the stored sperm. Researchers believe that "sperm competition" is likely in this scenario, as sperm from multiple males compete with each other for access to the egg. In fact, male bats from species that display delayed fertilization have larger testes than comparable bats, suggesting that producing more sperm has been selected for.

Due to the energy needed to ovulate and then sustain early pregnancy, often in advance of ample available insects, females must reach the end of hibernation with more intact fat stores than males. Thus, females are said to be "thriftier" with their energy stores during hibernation than males, altering their arousal patterns and torpor temperatures to conserve precious resources.

GIVING BIRTH MORE THAN ONCE

In more tropical environments, bats may be "polyestrous," giving birth twice per year, or in exceptional circumstances, more than twice. Most polyestrous species still give birth to only one pup at a time, but the Southeast Asian Least Pipistrelle (*Pipistrellus tenuis*) is an exception and may be the most fecund bat—giving birth to twins up to three times per year.

← Male Little Brown Myotis may mate with torpid females during hibernation.

↗ Some tropical bat species, like Peters's Lesser Epauletted Fruit Bats (*Epomophorus pusillus*), can give birth twice or more per year.

Some bat species that give birth more than once per year must overcome the normal hormonal signals that suppress ovulation during lactation. Sometime after birth they become sexually receptive, ovulate, and become pregnant again, all while still nursing their young. This pattern of biannual birth pulses and a postpartum estrus is common in the epauletted fruit bats, and is also sometimes present in the Egyptian Rousette.

In the Little Epauletted Fruit Bat (*Epomophorus labiatus*), timing is tied to the Afrotropical rainy season, with the first birth occurring at the start of the rainy season and the second birth near the end. After the first birth, ample food resources exist to support pregnancy while the female is still lactating, but some bats may fail to get pregnant again after the second birth, when food resources and thus their body condition are waning and they still need to make milk for the second baby.

In the same region, free-tailed bats in the genus *Mops* also exhibit polyestrous cycling with a postpartum estrous, with estimates of up to five births per year (which may be inaccurate). As we will see in the next chapter, giving birth more than once per year may be a key factor in the connection of these bats with Marburg and Ebola viruses.

Baby on board: pregnancy

Pregnancy is one of the most energetically expensive activities undertaken by a female. Once mating, ovulation, and fertilization have occurred, bats can control when pups are born by varying the number of days between fertilization of the egg and implantation of the embryo in the uterine wall. They can also alter the rate of fetal growth during pregnancy, taking longer to grow the baby if conditions make this necessary.

The length of gestation, or pregnancy, varies between and within bat species. Gestation length and developmental patterns are well studied in many (but not all) bat species, and the dominant theme that emerges for this most costly and evolutionarily critical activity is one of reproductive flexibility. Bat pups typically weigh between 20 and 30 percent of the mother's body mass at birth, which is made possible by the fact that the pelvic girdle is unfused in bats, permitting the passage of large young. To put this in perspective using a human analogy, this is the equivalent of giving birth to a human infant weighing 27–41 lb (12–19 kg), which is simply impossible.

Each pregnancy, especially for those species that twin, represents an extraordinary effort on the part of the female. Female bats must consume significantly more food than normal to sustain fetal development,

← Flying while pregnant requires extra energy and females, like this Northern Myotis (*Myotis septentrionalis*), must increase foraging time.

↗ This obviously pregnant Orange Nectar Bat (*Lonchophylla robusta*) must deploy hovering flight while pregnant in order to feed.

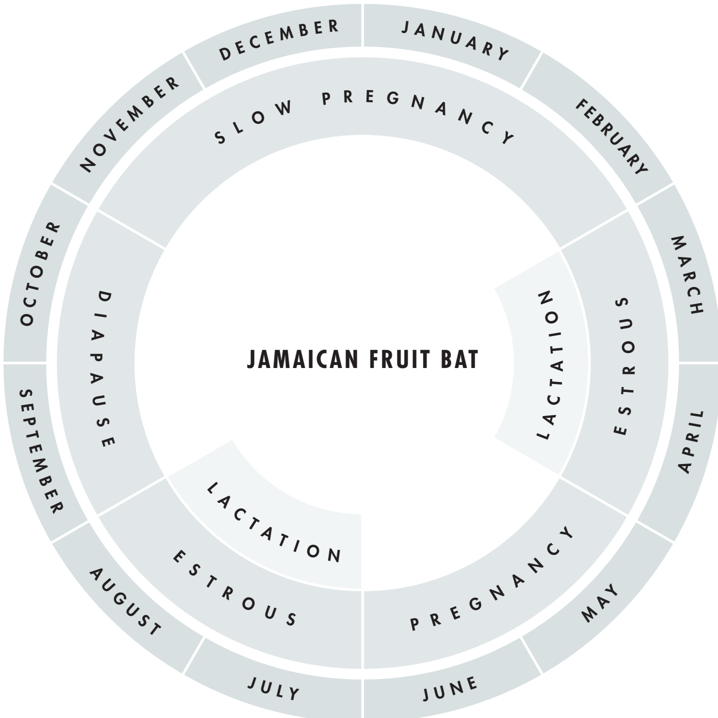
and they must do this while flying. Thus, their reproductive costs multiply as they need to consume extra calories both for their baby's growth and to support the increased costs of flying as a heavier animal. Late-stage pregnant bats are so large that they lose flight maneuverability and may be at greater risk of predation.

PRESSING PAUSE

Unlike the temperate hibernating bats that delay fertilization, a number of bat species hit the pause button at the next stage—halting development of the embryo, typically prior to implantation in the uterus. Termed embryonic diapause, these evolutionary reproductive decisions typically time reproduction, with its associated costs, to coincide with periods of peak food availability. For example, within the insectivorous bent-wing bats (*Miniopterus*), Schreibers's Long-fingered Bat in its northern ranges may delay implantation by as much as five months, waiting until the start of summer for implantation and proper gestation. In contrast, fetal development in bent-wing bat species in the tropics, where food is more widely available, begins immediately after mating.

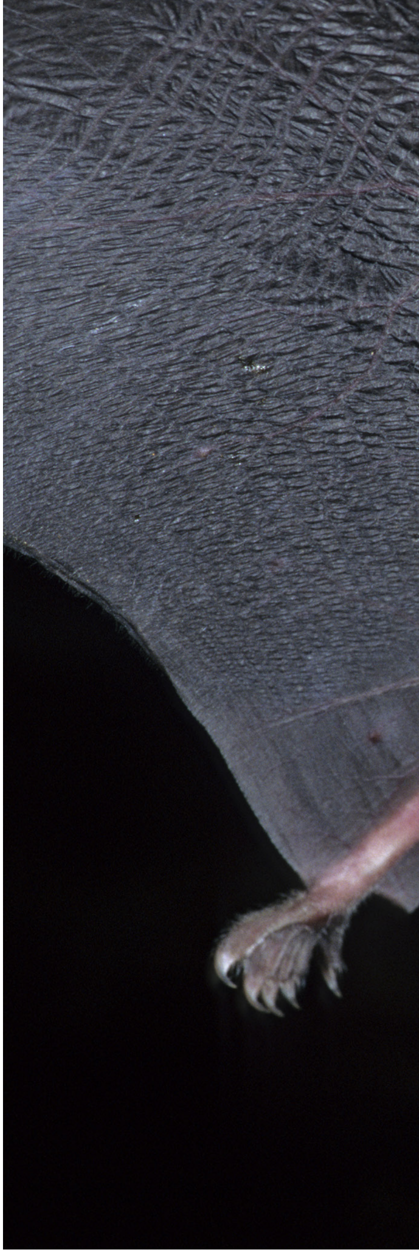
↑ In its northern range, Schreibers's Long-fingered Bat males and females synchronize reproduction. After fertilization of the egg, implantation of the developing early-stage embryo will be delayed by up to five months.

In a number of New World phyllostomid bats, such as the Jamaican Fruit-eating Bat (*Artibeus jamaicensis*), diapause occurs, but only after the embryo implants in the uterus, becoming dormant for up to ten weeks (see page 196). In this sense, it is an intermediate pattern between true delayed implantation and the final type of reproductive slowdown in bats—delayed development. In this scenario, bats can vary the length of pregnancy, developing their young more slowly. Typically seen in hibernating temperate bats (many of which already exhibited delayed fertilization), with a normal pregnancy of approximately six weeks, bats may increase the length of gestation by one-third or more if they experience a cold spring or early summer and decreased food availability.



Jamaican Fruit Bat annual cycle

This species gives birth biannually. Shortly after birth, while mothers are nursing their pups, females ovulate and are ready to mate again (estrous). Leading into the dry season (starting around September), females halt development of the embryo (diapause) after implantation in the uterine wall. Once development begins again, the pregnancy is long and slow, with birth occurring early in the rainy season. The subsequent pregnancy develops within the rainy season and is not prolonged.



Under conditions of low food availability, bats use daily torpor, decreasing their metabolic activity to conserve energy. By decreasing metabolic activity, the rate of fetal development is similarly decreased. Bats deploying this strategy are classified as "income breeders" for their ability to spend energy as it comes in to develop their pups and to halt development when food is less available. Although this strategy of gestation length flexibility allows bats to make the best of a bad situation, studies in the Little Brown Myotis have shown that later summer births translate to less growth and less time to fatten up before winter on the part of the pups—which significantly decreases their likelihood of surviving the first winter.

No matter the timing, bat pups are nourished by the mother through the placenta, connecting them to the mother's blood supply through the uterine wall. As described on pages 26–29, building a bat requires the unfolding of a unique series of developmental events within the bat uterus.

If implantation or the pregnancy otherwise fails, the reproductive system resets. In highly seasonal species, females may have to wait an entire year before they can try again.

↑ Female Jamaican Fruit Bats give birth to exceptionally large babies that hold on in flight by attaching to the nipple and gripping the mother's fur with their feet.

Birth, lactation, and parental care

After their sometimes long journey from fertilization to birth, bat pups still have much to do. Nourished by their mother's milk, bats must grow quickly, learn to fly, develop their echolocation skills, learn which food items are best and how to catch them, understand the spatial relationships between their roosts and their foraging sites, and develop the social skills needed to be a part of a colony.

← A female Egyptian Rousette, like most species, gives birth to a nearly hairless pup with its eyes closed.

↑ Bat pups, such as this Gray-headed Flying Fox baby, spend significant amounts of time with their mother, nursing and learning all there is to know about surviving in the wild.

The majority of bats studied give birth in a head-up or a cradle (horizontal) position, using the tail membrane and wings to cradle the baby during birth. The pups of most bat species are born naked and with their eyes closed, but fur begins to grow quickly and their eyes open within a few days. All bats are born with their deciduous "milk teeth," which allow them to attach securely to the nipple.

Lactation, the provisioning of carbohydrates, protein, fats, and antibodies to young in the form of milk, is even more energetically expensive than pregnancy. In the Little Brown Myotis, energy costs for milk production double during peak lactation, further burdening the mother.

Lactating bats may forage closer to the roost and in more frequent and shorter bouts than when pregnant or non-reproductive, presumably to facilitate nursing their young. Dietary shifts in lactation have been documented in some species, like the Asian Particolored Bat (*Vespertilio sinensis*), which preferentially select more nutritious insects at this time.

Most mothers leave their young in the roost while they forage, but in some species the pup may be carried by the mother on foraging trips or carried by her between roosting sites.

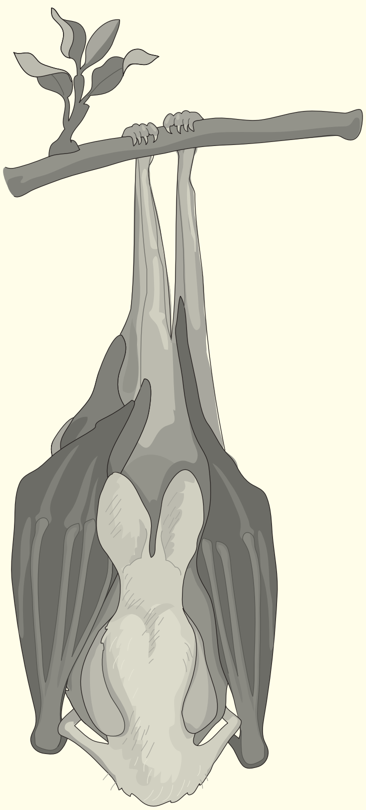
→ Energetic demands increase after giving birth, as bats like this Egyptian Rousette may carry their young while nursing.

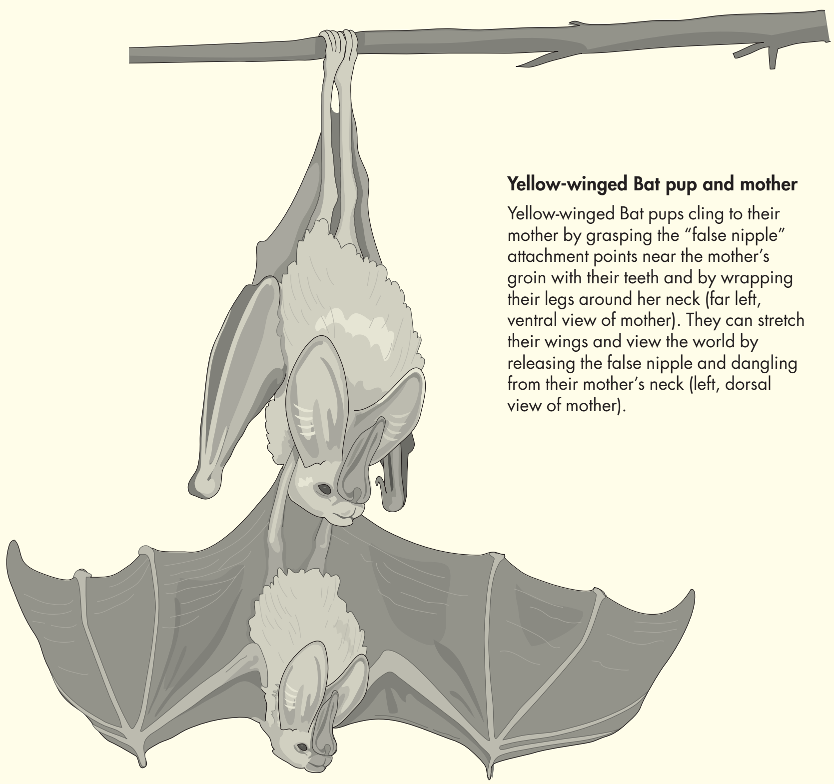
BABBLING BATS

Baby bats must develop the ability to produce echolocation calls and vocalizations used for communication. Recent work with the Greater Sac-winged Bat (right) demonstrated that pups in the roost produce a variety of repeated sounds or "syllables" that may help them hone sound-producing skills as they age. These sounds bear a striking resemblance to the babbling of human babies, in which simple syllables are repeated, like "babababababa." Practicing sounds needed later in life likely enhances their abilities to communicate with potential mates in the future.

TYPES OF NIPPLE

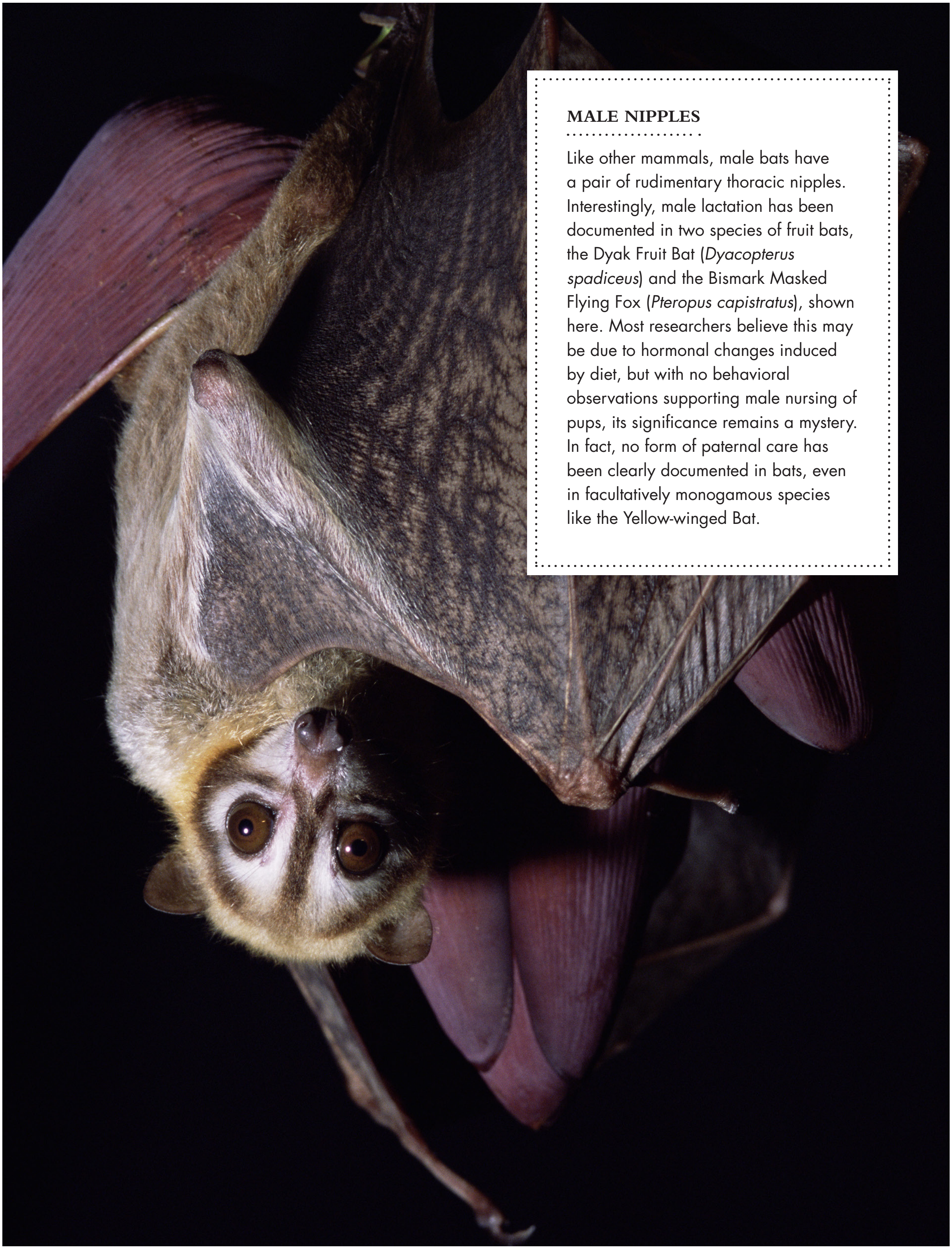
Nearly all bat species have one pair of thoracic nipples, but a few species that regularly twin have a second pair. Bats from a handful of families have a pair of "false" or inguinal nipples in the pelvic region. These are mostly used as attachment points. For example, the pups of the Yellow-winged Bat cling to their mother by holding the inguinal nipple in their mouth, wrapping their legs around her neck, and clutching the back of her neck with their feet.





Yellow-winged Bat pup and mother

Yellow-winged Bat pups cling to their mother by grasping the "false nipple" attachment points near the mother's groin with their teeth and by wrapping their legs around her neck (far left, ventral view of mother). They can stretch their wings and view the world by releasing the false nipple and dangling from their mother's neck (left, dorsal view of mother).



MALE NIPPLES

Like other mammals, male bats have a pair of rudimentary thoracic nipples. Interestingly, male lactation has been documented in two species of fruit bats, the Dyak Fruit Bat (*Dyacopterus spadiceus*) and the Bismark Masked Flying Fox (*Pteropus capistratus*), shown here. Most researchers believe this may be due to hormonal changes induced by diet, but with no behavioral observations supporting male nursing of pups, its significance remains a mystery. In fact, no form of paternal care has been clearly documented in bats, even in facultatively monogamous species like the Yellow-winged Bat.

GROWING PUPS AND PARENTING

Some of the best data on pup development come from the well-studied Greater Horseshoe Bat (see page 176). After rapid growth during the first three weeks of life, bats are almost as large as adults and have nearly fully developed wings. Young can fly in as few as 15 days and are competent fliers at 24 days. Although they continue to nurse for another 3 to 4 weeks, they are rapidly learning how to navigate their world, facilitated by the neural development that underlies echolocation. Like many bats, females from this species aggregate in large maternity colonies, nearly exclusively composed of pregnant females.

Allonursing, or the feeding of other females' pups, is extremely rare in bats, although babysitting other females' pups while a mother is foraging has been documented in several species. Even in species that roost in the thousands, mothers use a variety of cues to identify their own pup for feeding. For example, in the crèches of the Brazilian Free-tailed Bat, which may contain millions of bats, mothers can find their young through spatial memory, smell, and social calls.

Communication between mother and offspring is key to their bonding. The mechanisms through which females teach their young how and where to feed are poorly understood, but some species will bring live prey (for example, insects or frogs) back to the roost for their young. Recent advances in telemetry, including the development of "proximity sensors," are transforming our understanding of how mothers and their young travel together during nightly foraging and how mothers can teach their offspring critical skills. The rapid assimilation of these skills ensures that the next generation will survive and reproduce themselves. Sexual maturity in bats can occur within a few months but is typically reached within one to two years.

↑ A Brazilian Free-tailed Bat crèche, where millions of babies eagerly await their mothers' return.

→ Bat pups have much to learn from their mothers, including this month-old Gray-headed Flying Fox testing out the air.

HYPSIGNATHUS MONSTROSUS

Hammerhead Bat

Largest African bat

SCIENTIFIC NAME	*Hypsignathus monstrosus*
FAMILY	Pteropodidae
DIET	Fruit, especially figs
HABITAT	Varied types of forest
CONSERVATION STATUS	Least Concern
WEIGHT	Female: 7.3–10.7 oz (207–302 g) Male: 10.3–14.8 oz (291–419 g)
WINGSPAN	Around 39 in (1 m)

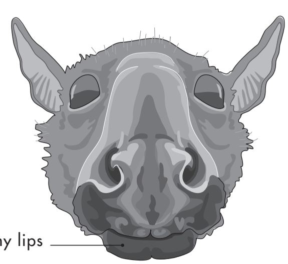
As a result of sexual selection inherent to their lekking behavior during mating, Hammerhead Bat males are nearly twice as heavy as females and have a larger snout with fleshy lips. No other bat species displays this much sexual dimorphism.

Hammerhead Bats roost in the forest canopy on exposed branches, camouflaged among the leaves. White fur patches at the base of the ears aid in breaking up their appearance when viewed from below. The muzzle of the female Hammerhead Bat is relatively simple, only slightly inflated relative to that of other African fruit bats. However, in males, the rostrum is literally hammer-shaped with a greatly expanded muzzle that ends in a flat, fleshy plate formed by both lips. The lips appear swollen and are covered with rugged skin and bumps.

The tongues of Hammerhead Bats are large with an expanded tip and backward-pointing papillae, which help in rasping soft fruits.

Female, young, and non-lekking adult male Hammerhead Bats forage nightly along regular routes, searching for continuously available (albeit low-quality) fruits, while displaying males forage later at night, flying farther to find higher-quality figs. As a result of needing to find fruit using both visual and olfactory cues, the pteropodid bat brain is big relative to the body size and compared with other bat lineages. Their visual centers and olfactory bulbs are larger than those of other bats, but their auditory centers are smaller due to the lack of laryngeal echolocation in this bat family. Unique to the pteropodid fruit bats, the wings of Hammerhead Bats have a claw on the second or "index" digit. They do not have a tail.

Female Hammerhead Bats give birth to a single pup twice per year. Since pregnancy lasts 5 to 6 months, having a second pup within a single year requires a postpartum estrus; females ovulate and are sexually receptive shortly after giving birth. Although relatively common across their range, Hammerhead Bats are persecuted for the noise they make while lekking and are hunted for food.



Face of male with fleshy lips

Male Hammerhead Bats have large fleshy lips and floppy jowls.

→ Hammerhead Bats are the largest bat species in continental Africa, easily identified by their appearance and size. This is a female, with a smaller rostrum than males.

LAVIA FRONS

Yellow-winged Bat

Ballet dancers

SCIENTIFIC NAME	*Lavia frons*
FAMILY	Megadermatidae
DIET	Larger insects, including beetles, moths, grasshoppers, and termites
HABITAT	Varied, semidesert steppes, tropical savannas, and open woodlands
CONSERVATION STATUS	Least Concern
WEIGHT	0.99–1.27 oz (28–36 g)
WINGSPAN	Around 14 in (35 cm)

Yellow-winged Bats hunt insects by hanging from a perch, swiveling their heads in all directions. With very large eyes, information from both vision and echolocation likely signals when to release their grip and fly to capture prey.

There are six species of bats in the family Megadermatidae, which share several distinctive features: large, oval ears that are joined above the forehead; a large, forked tragus within the ear; and a well-developed nose leaf. The tail and wing membranes are broad, hence the name *mega* (large) and *derma* (skin). Each of the six species is distinct enough to be placed in its own genus—the relationships between them are poorly understood.

Monogamous pairs of Yellow-winged Bats roost in the open, especially in acacia tree branches, which makes them susceptible to predation by raptors. The wing membranes, ears, and nose leaf are yellowish to yellow-brown in color, accented by long, woolly, gray fur which is darker on the back than on the front. This lighter coloration may provide camouflage in the open roosts favored by this bat.

Male Yellow-winged Bats have a gland on their lower backs from which exudes a yellowish secretion. This is possibly an attractant for females or a substance used to mark their territories. Courtship includes males and females swooping and circling around each other in an aerial ballet. Females give birth to a single pup once (but possibly twice) per year, just before the rainy season when food becomes more abundant. They may hunt opportunistically during the day and actively start feeding about 30 minutes before sunset.

→ Because of their preference for roosting in open canopy trees, Yellow-winged Bats are easily spotted across West, Central, and East Africa.

TAPHOZOUS NUDIVENTRIS

Naked-rumped Tomb Bat

Historical visitor

SCIENTIFIC NAME	*Taphozous nudiventris*
FAMILY	Emballonuridae
DIET	Beetles, moths, and other insects
HABITAT	Variable, including arid and semiarid regions, and forests
CONSERVATION STATUS	Least Concern
WEIGHT	1.06–1.23 oz (30–35 g)
WINGSPAN	Not known

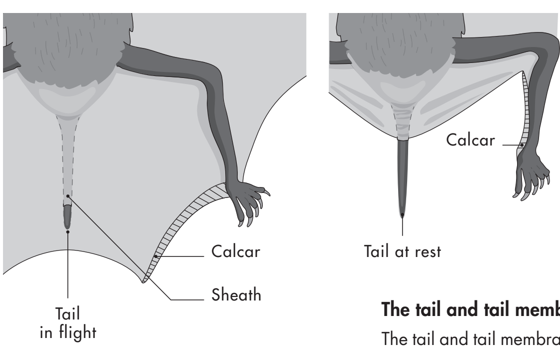
The Naked-rumped Tomb Bat is a medium-sized, grayish-brownish bat with no fur on its rump, lower belly, and hind limbs. These bats have long, narrow wings, fly very fast, and can forage more than 110 yards (100 m) above the ground.

The Naked-rumped Tomb Bat is a member of the family Emballonuridae, the sheath-tailed bats. They have unusual tails protruding from the upper surface of the tail membrane and enclosed in an elastic sheath. The tail membrane is able to slide along the tail from its base to its tip, thereby changing the shape and area of the tail membrane and providing enhanced maneuverability in flight.

Like many of the bats that the International Union for the Conservation of Nature (IUCN) classifies as being of "Least Concern," the Naked-rumped Tomb Bat is widely distributed, common in much of its range, thrives in multiple types of habitat, and tolerates a fair amount of habitat modification. Its diet includes beetles, crickets, grasshoppers, cockroaches, moths, and winged termites.

Some populations of the Naked-rumped Tomb Bat hibernate while others migrate. During the day this species roosts in narrow fissures and crevices between rocks or stone blocks. It is well documented occurring in old ruins, mosques, and the ancient Egyptian Nile Valley temples and tombs, including the famous Karnak Temple Complex. Due to the volatile secretions from the wing sac glands, presumably used in courtship, colonies of this species are known for their specific odor.

This species gives birth to a single pup each year in large maternity colonies. Unusual among bats, young Naked-rumped Tomb Bats have been recorded clinging to their mother's back within the roost.



The tail and tail membrane

The tail and tail membrane (uropatagium) from the dorsal side in flight (left) and relaxed (right); portions of the tail that are within the sheath are inside of the dashed lines. The calcar supports the extended uropatagium in flight.

→ Tomb Bats roost with their bellies or ventrum pressed against a surface, often leaving stains from urine and various glandular secretions.

VESPERTILIO MURINUS

Particolored Bat

Mother of twins

SCIENTIFIC NAME	*Vespertilio murinus*
FAMILY	Vespertilionidae
DIET	Variable, Diptera and moths
HABITAT	Extremely variable
CONSERVATION STATUS	Least Concern
WEIGHT	0.39–0.85 oz (11–24 g)
WINGSPAN	10–13 in (27–31 cm)

The Particolored Bat is named for its luxurious dorsal fur, red to dark brown with silvery prostate tips; its contrasting ventral fur is white to gray. Wings are dark brown and narrow.

This widespread and adaptable species is known from the northern Palearctic, ranging from France, Britain, and the Netherlands in the west through northern, central, and eastern Europe and Siberia to the Pacific coast. The Particolored Bat forages in open areas across a variety of habitats, including forest, steppe, semi-desert, agricultural, and urban environments. A hibernator, this species roosts in the winter in rock fissures, crevices in tall buildings, tree holes, and the occasional cellar. Although some populations are sedentary, migrations of up to 1,100 miles (1,780 km) have been recorded. Some Particolored Bats have occasionally been found on North Sea oil rigs and ships.

During the summer, bats may continue to roost in rock crevices or hollow trees, but may also be found in buildings or nest boxes. Unlike some other species of *Vespertilio* that may form maternity colonies that number in the tens of thousands, the Particolored Bat lives in small colonies and single individuals are sometimes sighted. In mid-summer, females give birth to twin pups, a divergence from the single pup born to most bat species. Females have been captured flying with their twin pups attached. In captivity, pups with greater access to food were found to reach sexual maturity up to a month and a half earlier than other pups, suggesting greater success for bats born in years with plentiful insects.

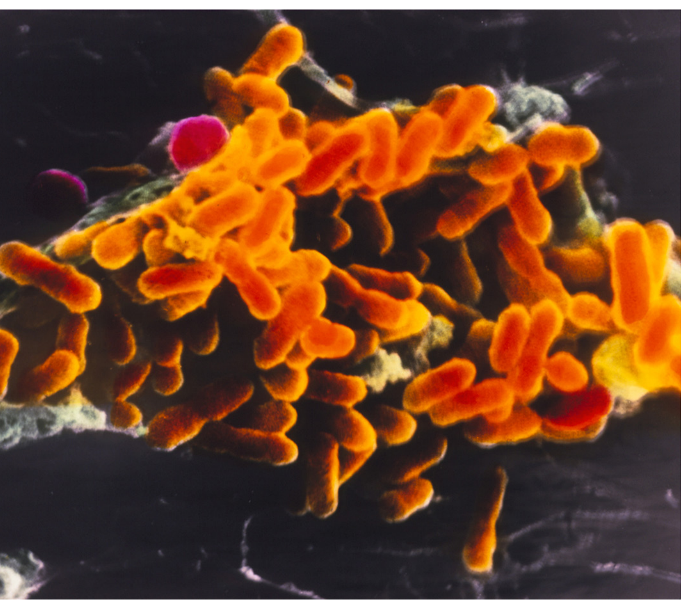
→ With its long, narrow wings, the Particolored Bat is a fast flier that forages in clearings and semi-open spaces.

IMMUNITY, HEALTH, & ZOONOSES

Bats and disease

All animals, including humans, harbor microorganisms that are sometimes pathogenic, meaning they cause disease. Bats have long been associated with disease, whether this is warranted or not. Balancing conservation and public health concerns is an ongoing effort with passionate scientists in each camp.

Within a One Health framework, in which the interconnections between animal health, ecosystem health, and human health are recognized, many scientists are studying bat diseases while simultaneously working to conserve bat populations. Microorganisms, or microbes, are those organisms that cannot be seen by the naked eye. Most microbes are tiny, single-cell beings, including bacteria and protozoan parasites, but fungi and the enigmatic "non-living" viruses and prions are also microbes.



The vast majority of microbes do not cause disease and some are even helpful—for example in aiding digestion. That said, some microbes are indeed harmful, ranging from being a nuisance to lethal. In some instances, microorganisms that have coevolved with their hosts over thousands of years are not pathogenic to them, but might be if spread to other species, including humans. When microbes from an animal like a bat spill over (are transferred) to people, they are called zoonoses.

Bacteria, found alone or in colonies, are important constituents of the bat gut and bat skin "microbiome," where they are most likely to be beneficial to their host. However, one bacterial lineage, *Bartonella*, is more likely to cause harm; infecting red blood cells, they can cause chronic illness in humans and other animals. Recent evidence analyzing the genetic sequences of *Bartonella* found in bats and other mammals suggests that bats are the ancestral hosts of all mammal-associated *Bartonella*—the source from which the bacteria radiated into other mammal lineages.

← *Rickettsia* species are small, Gram-negative bacteria that infect animal cells and can cause spotted fever disease.

↗ Bat flies, most of which are not this large, are wingless ectoparasites of bats that resemble spiders but only have six legs. This diverse group of animals spend nearly their entire lives feeding on bats' blood.

Spillover risk is assumed to be low, but a handful of examples of human infection with bat-borne *Bartonella* strains have been documented, including those likely acquired through the hunting and consumption of bats. *Bartonella* transmission from animal to animal occurs through hematophagous (blood-sucking) arthropod vectors. Like other animals, bats are plagued by multicellular macroscopic (visible to the human eye) parasites such as mites, ticks, fleas, and an especially egregious ectoparasite lineage—the bat flies. These arthropod vectors carry other bacteria besides *Bartonella*. For example, *Rickettsia* bacteria, in the spotted fever group, have been documented in ticks that feed on both bats and humans. Finally, arthropods can carry other pathogens, including the parasites that cause tropical diseases like malaria and Chagas disease.

BAT IMMUNITY

Bats have interesting roles to play in the evolution of microrganisms, but by and large do not appear to be significantly impacted by them. This is a common theme: there are very few examples of disease in bats. Although we have insufficient data on what constitutes a healthy bat, even those with high parasite or even high viral loads appear to head out to forage each night. Researchers are increasingly convinced that the relationship between bats and their pathogens may be different from that of other animal groups. The bat immune system and its regulation may be uniquely suited to fight (or perhaps to just ignore) infection, especially of intracellular parasites like viruses (see pages 226–227).

Like other animals, bats carry many viruses and the more we look, the more we find, most with little to no evidence of zoonotic potential. Rabies, perhaps the most notorious, has strong ties to bats and can kill them, but can also be hosted by any mammal.

Despite the diversity of viruses discovered in bats (who perhaps have been unduly singled out for study), less than a handful of other viruses are documented to actually harm them. One of these is the Tacaribe virus from the southern Caribbean island of Trinidad, which can be fatal to Jamaican Fruit-eating Bats (*Artibeus jamaicensis*). Perhaps more troubling are the repeated die-offs of thousands of Schreibers's Long-fingered Bats in Europe, most certainly from infection with Lloviu virus, a recently discovered filovirus most closely related to the suite of viruses in the genus *Orthoebolavirus*. There is no evidence of spillover to humans from Lloviu virus.

Finally, the pathogenic potential of fungi and fungal zoonoses, long ignored by science, is receiving increased attention. For bats, this amounts to a sad story of the most significant and ongoing mass mortality ever documented in wildlife, White-nose Syndrome, which is addressed in the next section.

↑ Mass die-offs from the Lloviu virus have occurred in Schreibers's Long-fingered Bats.

→ The Jamaican Fruit-eating Bat is highly susceptible to Tacaribe virus but can survive a low-dose infection.

White-nose Syndrome

Fungal infections are often considered only a problem for animals, including humans, that are immune-compromised. Bat conservationists and researchers were thus surprised to learn that a newly discovered fungus was to blame for the death of millions of North American bats, beginning in 2006.

White-nose Syndrome (WNS) is a disease of free-ranging hibernating bats in North America, which was first noted in New York State in 2006. Its name derives from the physical appearance of bats afflicted with the disease, in which white fungal growths occur on the nose and face. When scientists discovered the fungus that is responsible, they named it *Geomyces destructans* for its ability to destroy bat skin tissue, including on the wings. After taxonomic revision the fungus is now known as *Pseudogymnoascus destructans* (or Pd for short). Pd infection spread rapidly in North America, killing millions of bats. It is considered one of the largest and deadliest wildlife disease outbreaks in known history. As of 2024, Pd has been documented in 40 US states and eight Canadian provinces.

Pd can persist on cave walls and spread from bat to bat within the same hibernaculum, even across species. Since its discovery in North America and prompted by observations of facial fungal growth (without mortality) in hibernating bats in Europe, researchers have discovered Pd in both Europe and Asia and believe that it has existed in those ecosystems for hundreds, if not thousands, of years. European bats are tolerant of the fungus, having coevolved with it and likely suffering their own mortality events in the past. The strain present in North America is most closely related to European strains and is likely to have arrived on the clothing of someone who visited caves in both places.

← Named for its appearance on a hibernating bat's face, the fungus that causes WNS does most of its damage to the bat wing.

↗ WNS can be diagnosed using long-wave ultraviolet light, where spots of fungal growth in the wing fluoresce yellowish-orange.

→ The Silver-haired Bat is one of the species unaffected by the fungal pathogen that has devastated bat populations across North America.

HIBERNATION CONNECTION

Pd is a psychrophilic fungus, a type of extremophilic organism that grows and reproduces in cold, humid environments; the mines and caves in which bats hibernate provide the perfect microclimate for this fungus, as does bat skin. It does not grow at normothermic active bat temperatures or infect animals that do not hibernate, including humans. Of the roughly 47 bat species in the United States and Canada, more than half utilize hibernation and are susceptible to WNS. Pd has been found on 20 bat species as of 2024, but does not affect all equally. Twelve species, including two that are Endangered—the Gray Myotis and the Indiana Myotis—and one that is Threatened, the Northern Myotis, have been confirmed with WNS. Pd has been found on an additional eight species, including the Silver-haired Bat (*Lasionycteris noctivagans*), without ill effect, suggesting that they will not be affected.

Bats that are hibernating have significantly lowered metabolic rates and suspend the allocation of resources to many physiological systems, including the immune system. Pd attacks bats in this state and significantly erodes their skin, especially in the wings, which normally play an important role in managing water and electrolyte balance during hibernation. As a consequence, bats arouse from deep torpor much more frequently than normal, which depletes stored energy and can result in starvation.

Alarmingly, bats with WNS may be found flying outside their hibernacula in the middle of winter, including during the day, and die on the landscape. Scientists are still working to understand how some species suffer less from WNS and why some do not appear to be susceptible at all. Part of the answer may lie in their different hibernation temperature preferences, as some species prefer to hibernate between 36°F and 39°F (2°C and 4°C), well below the preferred temperature range of the fungus that causes White-nose Syndrome.

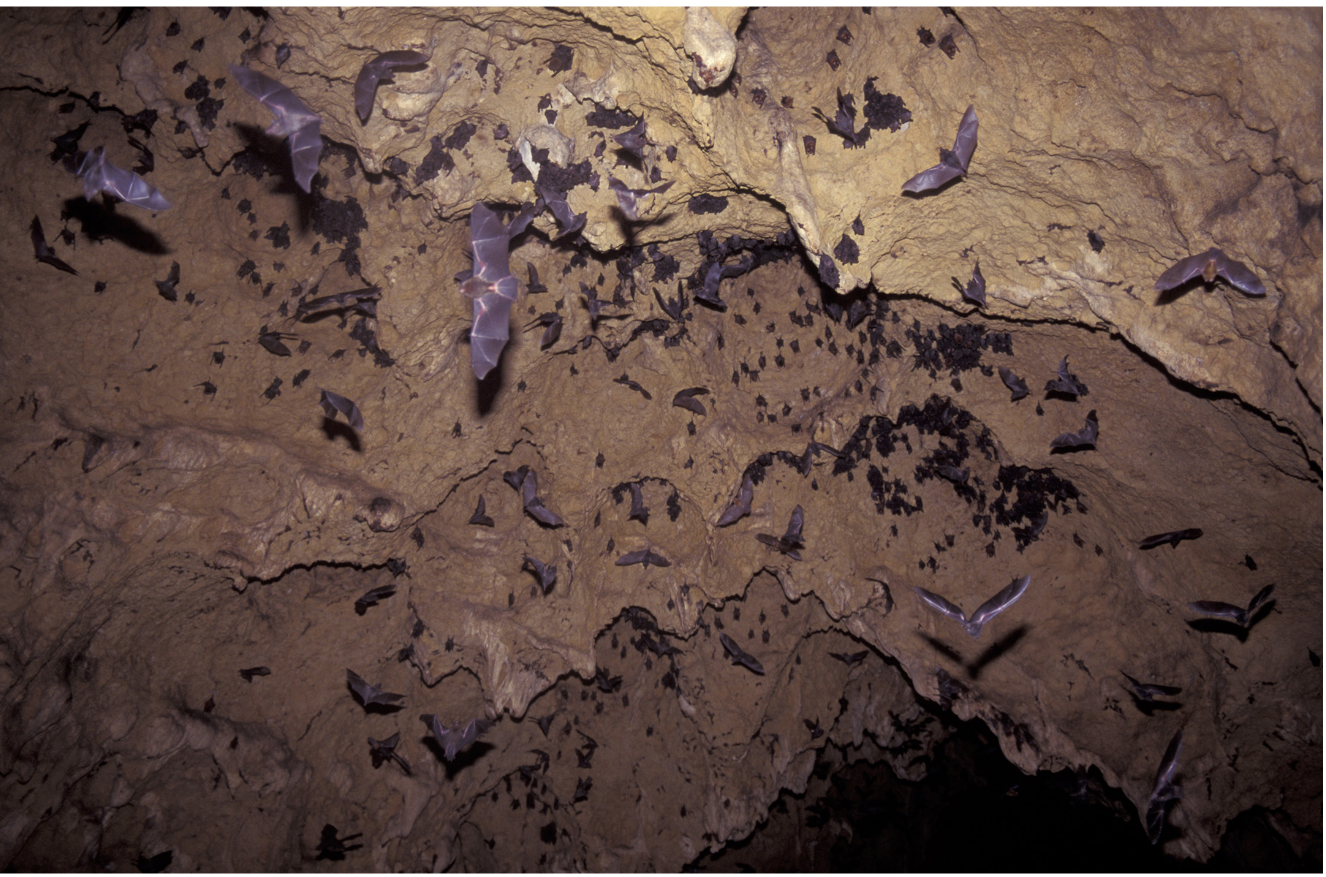
FIGHTING BACK

Some species also mount a more successful immune response to the Pd pathogen. Fortunately, there is hope on the horizon as researchers continue to work earnestly on this crisis. Evidence suggests that surviving bats do not show the too-frequent arousals from hibernation and are at lower risk of dying. Bats that live in colder hibernacula are also more likely to survive and trials that manipulate the temperature of hibernacula like mines in order to produce colder roosting sites are underway. Finally, laboratory and field-based testing of both treatments and vaccines are ongoing, and show promising results.

→ The Big Brown Bat mounts a successful response to infection with the pathogen that causes White-nose Syndrome and is thriving in regions where other species have declined.

The bat immune response

With the exception of White-nose Syndrome and a few viruses, bats appear largely unaffected by pathogens. A number of non-mutually exclusive ideas have been put forward to explain these bat superpowers, which may vary by species. But it is clear that these aspects of bat immunity have evolved over millions of years, in tandem with the evolution of other specific traits like flying and thermal plasticity.



One somewhat controversial idea, known as the "flight-as-fever" hypothesis, posits that the high temperatures exhibited by bats during flight decrease viral loads by controlling pathogen replication. This is known as immunological resistance and may be seen when a bat is early in its coevolutionary relationship with a given pathogen. The intriguing possibility is that, by controlling pathogen load but not completely eliminating a pathogen during these febrile bouts, selection for viruses that can persist within a bat at high temperatures translates to high pathogenicity when these viruses spill over to other hosts, like humans.

Consensus seems to be forming around the idea that bats are exceptionally good at immune tolerance: the ability to limit the health impact of a given pathogen burden. In this scenario, pathogen levels may reach peak levels, similar to those that would cause significant harm or even death to novel hosts like humans, but without significant health impacts to the bat. Bats may display tolerance to certain types of pathogens in general, but tolerance is the expected outcome when a given bat has coevolved with a specific pathogen for a very long time.

BALANCED RESPONSE

Perhaps the most important immunological trait exhibited by bats in the face of pathogens is balance. They appear to have the ability to both respond to pathogens to keep them in check and to minimize the health impacts of that pathogen (tolerance). For example, a number of bats appear to either constitutively express interferon molecules (chemical messages that "interfere" with viral replication), or be primed to respond strongly when stimulated.

←↗ In an initiative called "Bat1K," researchers are sequencing the genomes of bats across the Chiroptera phylogenetic tree, with a goal of characterizing the DNA of 1,000 bat species. Sequencing poorly known bat species, like the funnel-eared bats (*Natalus sp.*), along with well-studied species, will help scientists understand bat immunology and bat evolution.

At the same time, they may reign in the inflammatory process. Indeed, when novel hosts like humans die from pathogens such as Ebola or SARS-CoV-2, an overly exuberant, "runaway" inflammatory process rather than the virus itself may be to blame; bats seem able to keep inflammation in check and we surely have lessons to learn from them.

Viral reservoir hosts

Bats are frequently described as hosting more viruses than other vertebrate groups. Studies of the relationships between several bat species and a handful of well-documented and highly pathogenic zoonotic viruses, including rabies, Hendra, Nipah, Marburg, and possibly Ebola, have led to broad viral surveillance of bats around the world.

Most bat disease ecologists maintain that viral diversity is high in bats, even if sampling efforts have been skewed (for example, because bats are more likely to be sampled than rodents). Evidence that various virus families, such as Paramyxoviridae (which includes long-recognized and familiar viruses like measles and mumps), originated in ancestral bats and radiated within them over evolutionary time supports the idea of a special relationship between bats and some viruses, as described in the previous section.

Related to this, bat species appear to share more viruses with each other compared to other taxa. To understand this, consider a given habitat with 12 species of rodents and 10 species of bats. Rodent species are less likely to share viruses with other rodents because they are not nesting together. Bats, however, regularly co-roost with other bat species, sharing space in a cave,

← Multiple species of bats often roost in the same site, like this cave in Kenya. Sharing roosts promotes the sharing of viruses across species.

↗ Some bat species, like these Malagasy Rousettes (*Rousettus madagascariensis*), roost in dense clusters of hundreds to thousands of bats. With such close proximity, viruses can easily transmit between individuals.

tree hollow, or other resting place. They may be physically in contact with each other, but at a minimum are close enough to spread gastrointestinal and respiratory pathogens (like coronaviruses) between individuals of different species.

The overwhelming majority of viruses identified in bats have little to no zoonotic potential, meaning there is no risk of spillover to humans. However, a handful of the viruses hosted by bats have exceptionally high case fatality rates upon spillover to us. These highly virulent bat-borne viruses are largely restricted to four viral families: Rhabdoviridae, Paramyxoviridae, Filoviridae, and Coronaviridae. When considering viral evidence from a given animal, understanding if that animal was incidentally infected or whether it is a true natural reservoir host (where the virus lives in nature) is paramount. In nearly all instances in which a bat species is determined to be a natural reservoir host for a given virus, the infection is asymptomatic and does little harm to the bat. This is presumably due to the immune tolerance that has arisen over time (sometimes thousands of years) as a particular bat species and a particular virus species coevolved. Viruses in these systems may persist in bats at low levels over time.

RABIES

Rabies and rabies-related lyssaviruses (in the family Rhabdoviridae) hosted by bats are unusual in that bats either clear the virus (99 percent) without any infectious shedding or develop fatal rabies disease (1 percent) and can transmit the virus. The prototypical lyssavirus, rabies occurs only in bats in the Americas, although it is prevalent in carnivores (both wild and domesticated) worldwide. Lyssaviruses are unusual in that they are transmitted through direct contact via a bite or scratch. After brief replication at the wound site, the virus enters the neuronal system and moves toward the brain to replicate, afterward spreading to the salivary glands. In humans, rabies is always fatal without intervention;

nearly 60,000 people die each year of rabies but 99 percent of these cases originate in rabid dogs. This profound disease risk can be mitigated with prophylactic vaccination for at-risk persons (like bat biologists and veterinarians) and post-exposure vaccination and antibody treatment for those who have potentially been exposed. Vampire bats can be a significant source of rabies in livestock and humans due to their sanguivorous nature in which they bite the host prior to feeding.

SOSUGA, HENDRA, AND NIPAH

Paramyxoviruses have been identified in many bat species around the world. Of these, three viruses cause human disease: Sosuga virus, with a single human case in 2012, and the re-emerging related viruses Hendra and Nipah (first identified in 1994 in Australia and in 1999 in Malaysia, respectively).

Sosuga virus is hosted by the Egyptian Rousette from sub-Saharan Africa and the henipaviruses by several species of flying foxes in the genus *Pteropus*—all in the Old World pteropodid family. While Hendra outbreaks are rare, Nipah continues to emerge, with mortality rates of up to 75 percent. The likelihood of outbreaks is heavily influenced by human activity and by the presence of non-native bridging hosts, as described in the next section.

MARBURG AND EBOLA VIRUS

Old World fruit bats also play an outsized role in the ecology of filoviruses. Feared by many, infections with Marburg and Ebola virus (first identified in 1967 and 1976, respectively) are restricted to the African continent (until they get on an airplane) and are characterized by severe hemorrhagic fever in humans, chimpanzees, and gorillas. The single species of Marburg virus has been intricately tied to the cave-dwelling Egyptian Rousette, which roosts in the thousands in caves and mines frequented by people. Careful experimental work has demonstrated how Marburg persists in this bat species, which is largely unaffected by it but nevertheless sheds the virus in its urine, feces, and saliva.

In contrast, scientists are still actively trying to understand which bat species (or other animals) serve as reservoir hosts for any of the four species of Ebola that cause human disease. Viral RNA for one of these

← The Indian Flying Fox is one of the known hosts for Nipah virus but also an important distributor of seeds from the fruit that it eats.

→ The Little Collared Fruit Bat is one of a number of species in which the genetic components of Ebola virus have been detected.

zoonotic Ebola species has been detected in several African fruit bats, including the forest-dwelling Franquet's Epauletted Fruit Bat (*Epomops franqueti*, page 234), the Hammerhead Bat, and the Little Collared Fruit Bat (*Myonycteris torquata*). Like the Egyptian Rousette, these bats gives birth twice a year. This introduces newly susceptible bats (weaned pups) into the population semi-annually, likely providing a continual source of new bats for the virus to infect.

CORONAVIRUSES

Last, but certainly not least, are the coronaviruses, from whence came the COVID-19 pandemic. Coronaviruses infect a broad range of hosts, including birds, mammals, fish, and amphibians; in non-humans, coronaviruses are largely gut pathogens. Each coronavirus species is, however, very host-specific, infecting a single animal species or group of species in the same genus.

SARS-COV AND MERS

Within the viral family Coronaviridae, several viruses in the genus *Betacoronavirus* can cause significant human suffering and mortality, including the severe acute respiratory syndrome viruses (SARS-CoV and SARS-CoV-2) and Middle East Respiratory Syndrome virus (MERS). While none of these viruses has been directly identified in bats, each one appears to have an evolutionary bat origin, meaning that, at some time in the past, the 2019 pandemic virus and the bat virus shared a common ancestor. Indeed, there are many SARS-related coronaviruses identified in bats; the closest bat virus to SARS-CoV-2 was identified in the Intermediate Horseshoe Bat (*Rhinolophus affinis*, page 240) in southern China. Like the paramyxoviruses and, to a lesser extent, Ebola virus, bridging hosts appear to play a role linking bat-borne and human infection.

Spillover: a human problem

In the bat-zoonotic virus systems just described, or even in those not yet discovered, bats are not to blame for the spillover of viruses to people. Becoming exponentially more common, spillover is most often the direct result of human activity.

Viral outbreaks from animal sources have risen significantly over the past century. While this can be attributed, at least in part, to advances in public health surveillance, scientists point to the rapid rise in the number of humans (roughly 2 million in 1930 and over 8 billion today) and attendant shifts in human behavior as the primary culprit.

The relentless destruction of natural habitat and the expansion of agriculture have dramatically altered the access pathogens have to humans. For example, spillover of both Hendra and Nipah virus, described in the previous section, is facilitated by bridging hosts that are not native to the bats' habitats. Australian flying foxes (in the family Pteropodidae), which have long coevolved with the Hendra virus, now shed viral particles in urine and feces from trees above horse paddocks. These bats also spit out unwanted fruit fiber, which may be consumed by others. Horses, which die quite dramatically from Hendra, then transmit the virus to people.

← The sale of bats for meat, as seen here in Indonesia, poses a risk for hunters and butchers, who handle the live animals and meat before it is cooked, risking infection.

↗ The sale of bats in live animal markets poses an even greater threat to human and animal health as pathogens can easily spread between stressed individuals whose immune systems are weakened.

The closely related Nipah virus has a similar story: only this time the bridging hosts are domesticated pigs. As with Hendra, pigs on large farms contracted Nipah from bats such as the Large Flying Fox living in nearby fruit trees. Direct bat-to-human transmission of Hendra or of this strain of Nipah virus has not been documented, highlighting the impact human-made change can have.

In addition to habitat destruction and industrialized agriculture, the use of bats for food poses significant spillover risk. Bushmeat, or "wild meat" hunting, poses risks to hunters and food preparers, and in our increasingly global society, pathogen spillover in a small village can quickly spread. Of even greater concern are live animal or "wet" markets, where animals of all sorts, wild and domesticated, are stacked in cages under stressful conditions, weakening their immune system. These markets sometimes include bats, or other potential bridging hosts that can transmit bat-borne viruses to people. It is from such a market that the SARS outbreak of 2002 and the ongoing COVID pandemic may have emerged.

EPOMOPS FRANQUETI

Franquet's Epauletted Fruit Bat

Honking bat

SCIENTIFIC NAME	*Epomops franqueti*
FAMILY	Pteropodidae
DIET	Fruit
HABITAT	Rainforest and rainforest-savanna mosaic
CONSERVATION STATUS	Least Concern
WEIGHT	Female: 2.15–4.59 oz (61–130 g) Male: 3.24–6.07 oz (92–172 g)
WINGSPAN	Not known

Franquet's Epauletted Fruit Bat is a forest-dwelling species from West, Central, and (marginally) East Africa. It was named for Dr. Franquet of the French Imperial Navy, who forwarded a specimen to the Muséum national d'Histoire naturelle in Paris, where it resides today.

Franquet's Epauletted Fruit Bat is a medium-sized African pteropodid bat, related to the Hammerhead Bat and to other African epauletted fruit bats in the genera *Epomophorus* and *Nanonycteris*. Males are larger than females, have white fur epaulets on their shoulders, and lips and cheeks that are fleshy and expandable. Like other fruit bats in the family Pteropodidae, they have relatively large eyes because they do not have laryngeal echolocation and rely primarily on sight for orientation and navigation. In the field, Franquet's Epauletted Fruit Bat can be distinguished from *Epomophorus* in the same areas by its shorter rostrum.

When feeding, Franquet's Epauletted Fruit Bats collect fruit from the forest canopy and hold it within their expandable cheeks while they fly to a nearby perch to consume it. Figs are a favorite. In tropical Africa there are typically two rainy seasons and this species times its biannual births so as to maximize fruit availability during lactation and the period in which young become volant and can feed themselves.

Unlike other species of epauletted fruit bats, this species roosts singly or sometimes in pairs. They form "exploded" leks, where males display to attract females and emit a honking call, but are not clustered so tightly as the Hammerhead Bat. Both their deep forest habits and biannual birth pulses have tied them to the epidemiologic patterns of Ebola outbreaks; viral RNA and antibodies against the Zaire strain of *Orthoebolavirus* (EBOV) have been detected in this species.

→ Franquet's Epauletted Fruit Bat is found largely in intact forests; it is less likely than the other epauletted fruit bats to roost in proximity to humans.

MYOTIS LUCIFUGUS

Little Brown Myotis

A model species

SCIENTIFIC NAME	*Myotis lucifugus*
FAMILY	Vespertilionidae
DIET	Aquatic insects
HABITAT	Temperate, forested areas near water
CONSERVATION STATUS	Endangered
WEIGHT	0.18–0.42 oz (5–12 g)
WINGSPAN	8.7–10.6 in (22.2–26.9 cm)

The Little Brown Myotis was once the most common bat species in North America, with a range that included most of Canada and the United States. Eastern populations have crashed in the past 15 years as millions of bats died from the fungal disease White-nose Syndrome.

As the quintessential "little brown bat," this species may be the most studied in the world. It is the subject of over 2,400 scientific articles and its biology and behavior are well understood (as evidenced by multiple references to the species throughout this book). If there is such a thing as a bat "model organism," one studied extensively to understand particular biological phenomena, with the expectation that discoveries made about it will provide insight into the workings of other organisms, the Little Brown Myotis fits the bill. Many a bat biologist, including this author, cut their teeth studying this beloved but otherwise nondescript small species.

The Little Brown Myotis is one of 139 species of bats in the genus *Myotis* (Latin for "mouse-eared"), which is the most diverse of any bat genus in the largest of the bat families, Vespertilionidae. Nearly one out of every ten bat species recognized today is a mouse-eared bat. Only the horseshoe bat genus *Rhinolophus* comes close, with 114 species. The Little Brown Myotis is an obligate hibernator that displays a dissociated pattern of reproduction and overwinter sperm storage and the delayed development of pups through the use of torpor when food is unavailable.

Tragically, this bat is one of the species most heavily impacted by the wildlife disease White-nose Syndrome. It is exceptionally susceptible to the fungal pathogen that causes this disease, although remnant populations in eastern North America may be stabilizing.

→ Female Little Brown Myotis Bats give birth to a single pup each spring. Although only about half of the pups survive their first winter, adult bats can live 30 or more years.

PTEROPUS VAMPYRUS

Large Flying Fox

Not a vampire

SCIENTIFIC NAME	*Pteropus vampyrus*
FAMILY	Pteropodidae
DIET	Fruit, flowers, pollen, and nectar
HABITAT	Lowland forest
CONSERVATION STATUS	Endangered
WEIGHT	1.5–3 lb (0.7–1.4 kg)
WINGSPAN	52–59 in (1.32–1.50 m)

The Large Flying Fox is among the biggest of bats, with a wingspan of nearly 60 in (1.5 m). Mostly dark brown to blackish, with some orange and red fur, its color may vary by age, sex, and subspecies. Its long, pointed ears help distinguish this species from similar bats.

The Large Flying Fox was first described in the 1758 publication *Systema Naturae* in which Carl Linnaeus named all known animals and formalized zoological nomenclature. Not surprising given its size and attention-drawing, gregarious nature, the charismatic Large Flying Fox was among the original seven known bat species at the time, recorded as "Vespertilio Vampyrus." In his notes, Linnaeus wrote "*Noctu haurit sanguinem dormientium*" (At night it draws the blood of sleepers), a clear reference to the mistaken interpretation of this fruit-eating bat's large canine teeth and the rationale for its name.

Large Flying Foxes roost in trees in a variety of habitats, with colonies that range from 50 to 20,000 individuals. Their preferred lowland forest habitats are fragmented across much of their historical range, but some individuals will inhabit less disturbed urban environments, including botanical gardens. Like other flying foxes, they eat fruit, flowers, pollen, and nectar.

This species is heavily persecuted and hunting occurs at most roost sites and foraging locations accessible to humans, regardless of the bats' legal protection status. In the past 25 years, the Large Flying Fox's global population size has declined by over 50 percent. Anthropogenic pressures, including agricultural expansion, have brought bats and people into greater contact. One unfortunate consequence is the zoonotic spillover of Nipah virus from Large Flying Foxes to domesticated pigs, which serve as bridging hosts and pass the virus to people.

Like most bats, female Large Flying Foxes give birth to a single pup each year; in captivity, weight at birth averages 4.7 oz (133 g), much more than adults from the vast majority of bat species. With such a slow reproductive rate, population recovery is challenging.

→ The majestic Large Flying Fox can travel up to 31 miles (50 km) per night in search of food, crossing large bodies of water to travel to neighboring islands.

RHINOLOPHUS AFFINIS

Intermediate Horseshoe Bat

Adaptable synanthrope

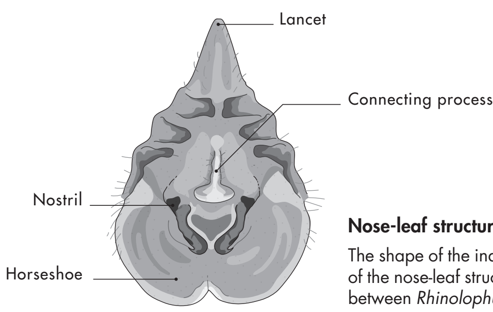
SCIENTIFIC NAME	*Rhinolophus affinis*
FAMILY	Rhinolophidae
DIET	Beetles and moths
HABITAT	Variable, cave-roosting
CONSERVATION STATUS	Least Concern
WEIGHT	0.35–0.67 oz (9.9–19 g)
WINGSPAN	Not known

The Intermediate Horseshoe Bat is a medium-sized Old World nose-leaf bat that is widely distributed in southern Asia, documented from northeastern India and Nepal to southern China, through mainland Southeast Asia to Indonesia.

This species is very adaptable and found in a variety of habitats. It occurs in primary forests (pristine, not previously disturbed), secondary forests (those regrowing from previous degradation), and disturbed habitats, including agricultural areas. In China it is found in the tropical eastern highlands and in both wet and more temperate western highlands.

The Intermediate Horseshoe Bat roosts in the thousands in caves. Like its relative, the Greater Horseshoe Bat, it feeds both by perch-hunting and by aerial hawking, consuming primarily moths and beetles. Female Intermediate Horseshoe Bats give birth to a single pup once per year in more northern ranges and twice per year in Peninsular Malaysia (and presumably other tropical areas within its range).

The rich species diversity of *Rhinolophus* bats in southern China and Southeast Asia, a known hotspot of bat diversity, may be tied to the viruses that circulate between and within them. Contact between different bat species, often through co-roosting in the same cave, increases the likelihood of viral sharing between them. Well before the 2019+ global COVID pandemic, a variety of SARS-related coronaviruses were identified in horseshoe bats in this region. Synanthropic bat species (those that readily live in close proximity to humans), like Intermediate Horseshoe Bats, are more likely to come into close contact with humans. They also may come into contact with other animals, including those found in live-animal markets, which could act as bridging hosts between bats and people. To date, the closest viral relative to the SARS-CoV-2 virus that causes COVID is coronavirus RaTG13, isolated from an Intermediate Horseshoe Bat in 2013. This virus's genetic code is 96.2 percent identical to that of SARS-CoV-2, suggesting a shared evolutionary history, but not a smoking gun.



Nose-leaf structure

The shape of the individual components of the nose-leaf structure help distinguish between *Rhinolophus* species.

→ The Intermediate Horseshoe Bat was first described from the island of Java and may represent a complex of closely related species. Further taxonomic study is needed.

ROUSETTUS AEGYPTIACUS

Egyptian Rousette

Tongue clicker

SCIENTIFIC NAME	*Rousettus aegyptiacus*
FAMILY	Pteropodidae
DIET	Soft fruits and flowers
HABITAT	Highly variable
CONSERVATION STATUS	Least Concern
WEIGHT	2.86–6.03 oz (81–171 g)
WINGSPAN	23.6 in (60 cm)

The Egyptian Rousette is widely distributed and found in abundance from South Africa to North Africa, through the Middle East up to Turkey and Southwest Asia into Iran and Pakistan. It has broad habitat tolerance and is at home in arid, moist tropical, and subtropical biomes.

This medium-sized fruit bat is an obligate cave rooster, with colonies of up to 50,000 individuals in parts of its range. Within the roost, bats hang in very densely packed clusters, continually shuffling around and noisily fighting to find the darkest corner or crevice. These squabbles even escalate to physical fighting, with bats punching each other with their thumbs and forearms, biting each other, and screeching.

This species, without laryngeal echolocation but with large eyes, can use vision to navigate above ground. Needing to navigate in the darkest parts of caves, however, led to the evolution of echolocation using clicking sounds, which Egyptian Rousettes produce with their tongues.

The physiology and behavior of Egyptian Rousettes is well studied, in part because they are easy to keep in captivity. Female Egyptian Rousettes give birth to a single pup either once or twice per year, depending upon habitat and food availability, although twins are not unheard of. The young are born with their eyes closed and their ears folded and are nearly naked at birth (see page 198). Approximately ten days after birth, their eyes open and their ears become erect and mobile. Within the roost, the young cling to their mothers, who fold their wings over their pup for protection, for about six weeks. At approximately 25 days of age the young bats stretch their wings and practice beating them, taking their first flights about 40 days later.

Likely tied to their highly gregarious and colonial nature, with bats packed tightly in the roost, this species has been documented to host two zoonotic viruses of consequence: Sosuga virus and Marburg virus. Cave disturbance and persecution occur in parts of its range, which exacerbate human–animal conflict and make viral spillover more likely.

→ The Egyptian Rousette is frequently encountered by both locals and tourists who enter cave and mine roosts. Curtailment of human visitation of these sites would reduce the risk of Marburg virus spillover in sub-Saharan Africa.

BATS & HUMANS

Ancient myths and modern views

People hold a variety of beliefs about bats, both positive and negative. Often mistaken for birds but rarely seen up close in a friendly setting, bats fall prey to our lack of understanding. Like other nocturnal animals, they are perceived in many cultures as disgusting or frightening. Yet in some cultures bats are regarded as auspicious and are even deified.

Representations of bats can be found in archeological artifacts from around the world. They are especially prevalent, even today, in China. Perhaps just by luck, the Mandarin Chinese word for "bat" is a homophone (pronounced in the same way) as the word for "fortune." The Five Fortunes—longevity, wealth, health and composure, virtue, and a peaceable death—are symbolized in the Wu Fu, which is typically depicted as a ring of five bats.

Bats also appear singly in Chinese imagery, usually shown in red, the color of joy. Bats are sometimes carrying money, flowers, or fruit, and even red swastikas. This imagery predates the Nazi period in Germany by centuries, and has positive connotations. In some dialects the word for 10,000 is the same as the word for swastika; in this context the appearance of a swastika represents 10,000 blessings.

↖ Each of the five bats in the Wu Fu circle represents one of the blessings of longevity. This motif is considered powerful and auspicious.

↗ In Mayan culture, the "death bat" Camazotz is a deity that served the lords of the underworld. Statues of Camazotz are common across the former Mayan empire.

On the other side of the world, the Mayan K'iche' people of Guatemala, deified bats. Unfortunately, the deity's name, Camazotz, means "death bat," and it served the lords of the underworld. Bat images can be seen today in the carvings on Mayan ruins, adjacent to live nose-leaf phyllostomid bats roosting in the cool inner chambers. Bat carvings also appear in association with Mayan tombs, likely because bats frequently roost in caves, which represented portals between the world of the Mayan people and the world of their gods. Preceding Mayan culture, bats were also mythologized by the Aboriginal people of southeastern Australia, who would have been intimately familiar with the large and conspicuous species of flying foxes. In this culture, the creator deity is a wedge-tailed eaglehawk known as Bunjil who had a bat for a brother, named Balayang. As the story goes, Balayang refused his brother's request to come and live with him. In retribution, Balayang's country was set on fire. In the melee, Balayang and his family were scorched and turned permanently black—thus providing a folkloric explanation for the color of bat wings.

Unfortunately, despite improving perceptions of bats in some places and contexts, fear and disgust regarding bats remain widespread. In one cross-cultural study, bats were ranked as more disgusting than cockroaches, spiders, maggots, worms, beetles, and leeches, and just slightly better than wasps, lizards, mice, rats, and slugs. Even kindergarteners classify bats as "bad." In India, the Wildlife Protection Act of 1972 classifies bats as vermin, excluding them from all manner of protection. Bats are associated with witchcraft in multiple African countries and even dead souls searching for rebirth in Europe. The myth of bats as vampires, only really true in the New World tropics where the three species of vampire bats live, persists around the world to this day.

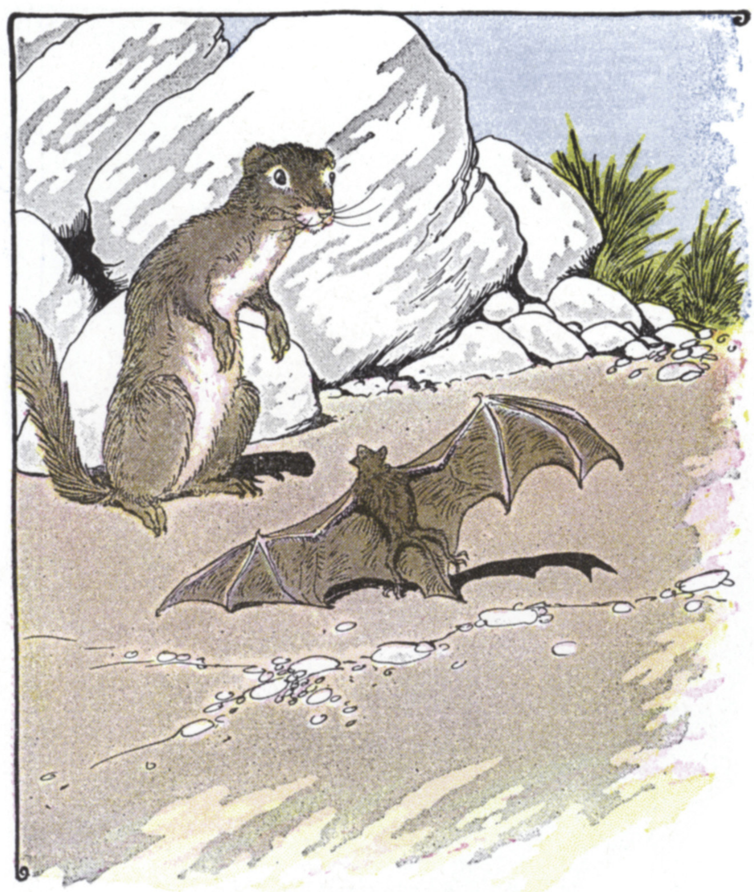
↑ Pura Goa Lawah (Bat Cave Temple) in Bali has bat ornaments inlaid with gold; multiple species of bats roost within this Hindu holy site.

→ As illustrated here, the crafty bat from Aesop's "The Bat and the Weasels" avoids being eaten by alternatively declaring himself to be a bird and a mammal.

CONFLICTING BELIEFS

One challenge for conservationists is that varying perceptions of bats exist, even within the same geographic region. For example, in northwestern Uganda, members of different tribes have different myths and perceptions of bats. In response to a recent survey, Lugbara tribe members universally claimed little knowledge of bats but relayed that they are messengers of death and witchcraft. In contrast, the Alur and Acholi people believe bats are wise animals and some Acholi believe that eating bats makes one intelligent. A Muganda, from central Uganda, relayed the following folktale: All animals used to pay tax to the Buganda king, but the bat played tricks to evade payment. Each time taxes were being collected from land animals, the bat claimed to be a bird, and when the time came to collect taxes from flying animals, the bat claimed to be a mammal, evidenced by its teeth. Their cunning deception is viewed as a lack of respect for the king and because of this, there is no need to conserve bats.

The notion that bats are tricksters or deceivers occurs in other cultural contexts as well. In two different fables from Aesop, "The Bat, Birds, and the Beasts" and "The Bat and the Weasels," a bat portrays himself alternatively as either a bird or mammal to avoid picking sides in a war or to avoid being eaten by a weasel. The moral of these stories—he that is neither one thing nor the other has no friends—epitomizes the conflicting views of bats that continue to this day.



Views on bats are not just cultural, but also religious. While the Bible describes bats as "detestable among the birds" and not to be eaten (Leviticus 11:13–19), a Shia Islamic text, the Shi'a hadith, portrays bats as a miracle of nature. Along with religious dictates, cultural taboos against harming or eating bats or destroying their roosts can be leveraged as tools for conservation. For example, the Antandroy and Mahafaly people of Madagascar hold taboos that prohibit them from eating bats and view some forests as sacred and thus to be protected. The sacred nature of some localities teeming with wildlife, including caves and religious sites like monasteries, are recognized by many peoples throughout the world.

DISEASE CARRIERS?

Although some innocuous bat myths, such as "bats get in your hair" and "bats are blind," persist to this day, other myths have the potential to cause real harm to bats. The biggest misperception right now is the sometimes sensationalistic portrayal of bats, writ large, as hosts of deadly viruses. As described in the previous chapter, bats (like all animals, including humans) play host to a variety of microbes. In a handful of bat-virus systems, these include viruses that are exceptionally virulent in humans. But the same could be said for other animal groups like primates, rodents, and water birds like ducks and heron.

Both the media and scientists need to be measured and precise in their descriptions of risk, which are sometimes very real, but can be mitigated. The consequences of alarmist language can be dire and even counterproductive. The broad perception that bats are dangerous and that spillover from bats poses a significant risk to humans increases the threat of culling (mass killing of bats) or roost-site destruction for all bats, as was seen all around the world following the initial days of the COVID-19 pandemic.

← A simple bamboo basket prevents bats from reaching date palm sap that is being collected for human consumption, thus reducing disease risk.

↗ Humans must learn to live safely with bats, including these Indian Flying Foxes that may carry zoonotic viruses.

Messaging about the disease risks of bats and other wildlife is important but runs the risk of characterizing bats and other wildlife as "epidemic villains," threatening their survival. Disease ecologists and conservationists must work together, along with public health officials, veterinarians, policy makers, and the like, to develop holistic solutions using a One Health approach (see page 218). In addition to mitigating the effects of habitat destruction, the prevention of spillover is the single most important solution to the risks posed by zoonotic pathogens.

EASY WINS

Sometimes simple solutions can have a large impact. For example, the strain of Nipah virus in India and Bangladesh is spread not by pigs as bridging hosts but by drinking date palm sap collected in jugs or clay pots. Bats, being more than happy to drink from these pots, contaminate the sap with Nipah virus by urinating and defecating in them. A simple, inexpensive solution was the local manufacture of bamboo baskets placed on top of the pots that prohibited bats from sampling their wares. A conservation win for bats and an epidemiological win for people.

Perhaps the most effective way to influence the perception of bats by people is to replace scary, negative emotions about them with warm, positive sentiments. Bat biologists, sociologists, educators, conservationists, and the press each has a role in turning the tide for bats by presenting them as the amazing beings they are and by dispelling myths about them. This can be done without ignoring the science underlying the disease risks of interacting with wildlife in general and bats in particular. Tailored for different cultures and settings, changes in perception start with children, who hopefully carry the message home to their extended families.

Ecological disturbance

Bats face myriad conservation threats, nearly all of which stem from human-made ecological disruption, including habitat degradation and loss, global climate change, and light pollution. Bat responses to these challenges range from decreased populations to local extirpation, shifts in distribution in response to altered food availability, and changes in behavior.

↙ Conversion of forest into agricultural land, especially for single crops like date palm, shown here in Thailand, poses significant conservation risks for bats and other animals.

→ The Large-eared Pied Bat is an example of a species threatened because it is naturally rare, making it even more susceptible to the effects of habitat loss.

Ecological disturbance in the form of habitat degradation (logging, mining, and fire), land-use change (conversion to agriculture), urbanization (conversion to densely populated areas, often with light pollution), and the extreme conditions brought about by global climate change (storms, droughts, and extreme heat) are the primary threats to bats worldwide.

Studies of the effects of ecological disturbance on bat populations universally show declines in population size and the local extirpation of certain species. This is especially true for bats with highly specialized diets and roosting requirements, as well as those more susceptible to stress from disturbance. For example, when flying foxes (family Pteropodidae) are energetically stressed by losing their source of nectar from winter flowers, the risk of spillover of Hendra virus from bat to horse (and then potentially to humans) is significantly elevated.

Bats that are generalists and less picky with regards to roosting and their feeding requirements, along with those species with total numbers in the hundreds of thousands (or even millions), are inherently more resilient than those with small numbers and restricted ranges. For naturally rare species, anthropogenic pressure can have outsized consequences. For example, the Hog-nosed Bat is known only from two geographically restricted populations in Thailand and Myanmar, estimated to contain just over 10,000 animals in total. This species, the smallest of all mammals, roosts in caves that are disturbed by religious visits, fertilizer collection, tourism, and limestone mining. Similarly, the Large-eared Pied Bat (*Chalinolobus dwyeri*, page 266), with less than five maternity roosts and a very restricted geographical range, is experiencing significant decline.

All that being said, with intervention and habitat restoration, some declines can be reversed and concerted conservation efforts can have significant impact. One must keep in mind, however, that bats, with their slow life histories, reproduce slowly and thus population recovery takes time.

Bats in buildings

One consequence of the relentless habitat destruction of the past century is that bat roosts are lacking. Being the adaptable creatures that they are, some bat species manage by roosting in just about any other suitable spot that meets their needs, increasing their likelihood of contact with people.

For bat species that are more flexible with regards to their roosting requirements and even their foraging needs, human-dominated landscapes will do in a pinch. Artificial roosts even allow some bat populations to thrive and reach numbers that previously did not exist. More likely to be used by cavernicolous (cave-roosting) bats than by tree-roosters, a variety of anthropogenic structures provide the microclimate and hiding places that bats prefer.

Discovery of bats in human-made structures can provide an opportunity for conservation, particularly when those structures are otherwise abandoned. For example, in southern India, hundreds of very old temples, built with granite stones and bricks, dot the landscape. Within these temples, some of which are still visited by people, temperatures are stable and warm, providing roosts for maternity colonies.

→ Bats are frequent inhabitants of older human-made structures, like the Underground Shiva Temple in Hampi, India.

↓ Bats, like these Mouse-eared Myotis, often colonize older wooden structures where rough-hewn lumber provides ample footholds.

Across the southern half of the United States and throughout much of Latin America, the Brazilian Free-tailed Bat is an especially common occupant of human-made structures. In the United States, they can be seen emerging nightly from the Congress Avenue Bridge in downtown Austin, Texas. The largest urban bat colony in the world, this site is a major tourist attraction and is estimated to contain 1.5 million bats, with an additional 750,000 pups born each year. This species can be viewed, with educational programming, at multiple sites in Texas, which hosts over 32 million free-tailed bats.

↓ Bat watching is a popular tourist activity in Austin, Texas, where 1.5 million Brazilian Free-tailed Bats roost under the Congress Avenue Bridge.

BATS AT HOME

Many adopted human-made roosts pose little problem for people, but bats are generally unwanted in personal homes. Thankfully, ample guidance exists for how to manage close encounters of the bat variety. Finding a single bat in your dwelling, which is likely confused or lost and didn't aim to be there, is rarely cause for alarm. When possible, close doors of adjacent rooms and open up windows (and window screens) and exterior doors. Turning off lights and ceiling fans inside and turning on lights outside (which may attract insects and thus bats) will help the bat find the exit. Stay calm and patient and keep your eyes on the bat, so you can be sure it has left your home.

For the bat that does not leave on its own, there are methods for safely capturing and releasing it without coming into direct contact with it. Bat Conservation International and other bat-focused organizations post guidelines on their websites for removing bats without directly handling them. If you suspect there has been direct contact between a member of your household and a bat, or cannot verify that contact (especially bites

↑ A bat condo in Ocala National Forest (Florida) can house thousands of bats, especially during the summer maternity season.

↗ The Perky Bat Tower in the tropical Florida Keys was built in 1929 in an attempt to attract bats that would eat the mosquitos that transmit malaria. On the US National Register of Historic Places, it was unfortunately destroyed in 2017 by hurricane Irma.

and scratches and especially in children) did not occur, contact your public health department and your physician, especially in the Americas, where the *very rare* bat may have rabies (see page 229).

PROVIDING ROOSTS

Colonies of bats can be safely removed, but as many species are protected, local and national guidelines must be followed. Reputable and licensed wildlife management companies exist that specialize in bat exclusion, which is typically performed after pups can fly. To accommodate bats that have been excluded from a dwelling, many home and business owners opt to erect a bat house (or even a bat condo) to provide shelter for bats seeking a new home. Frustratingly, these houses sometimes remain unoccupied, but following regional guidelines on their placement, design, and paint color can increase the likelihood of habitation.

International guidelines vary, but in the United Kingdom and much of Europe, all bat species and their roosts are protected—including bats that have roosted in buildings. In these places people have learned to live with bats, facilitated by concerted efforts to demystify bats and their behavior. In some instances, architects even accommodate bats by building special bat lofts for roosting bats within an existing roof structure. As we will see in the next section, living safely with bats, in the local and global context, is a key conservation and public health goal.

Global conservation

As highlighted throughout this book, each bat species is dependent not only on set food resources but also on particular roost types, both of which may vary across seasons. Some species are more adaptable than others, but many occupy very specific niches. Conservation efforts thus primarily focus on protecting where bats eat and where they sleep.

Over a third of bat species are Endangered, Threatened, or we simply have no information available to assess their conservation status. Over half of all species either have decreasing population trends or insufficient data to gauge the current status of populations. Put together, the combined number of species in need of conservation research or action exceeds 80 percent of all known bat species. This mind-boggling statistic emerges from the inherent challenges of studying secretive nocturnal animals that live in exotic places, but also from the global lack of dedicated resources.

→ Straw-colored Fruit Bats are highly adaptable and resilient, yet still face threats from habitat loss, hunting, and persecution.

For the largest of the Old World fruit bats (81 species in *Pteropus*, *Acerodon*, and related genera, most from islands), hunting for food and the killing of bats considered a nuisance to fruit farms pose profound conservation risks. Many of these bats are on the brink of extinction and six have recently gone extinct due to hunting pressures and persecution. Two Critically Endangered species—the Pemba (island) Flying Fox (*Pteropus voeltzkowi*) and the Rodrigues (island) Flying Fox (*P. rodricensis*), although still threatened, have been brought back from the brink only through concerted conservation action.

BAT CULLS

Exemplifying the extreme threats faced by Old World fruit bats today, the Greater Mascarene Flying Fox (*Pteropus niger*) is under persecution not by actors in the illegal wildlife trade but by the Government of Mauritius, which authorized several government-implemented mass culls of tens of thousands of bats based upon the belief that they damage crops, when data suggest birds do more harm. The population has likely declined by more than 50 percent since 2015. Currently listed as Endangered (2024), it may soon be listed as Critically Endangered.

↑ Fruit trees can be covered in nets to keep both birds and fruit bats from destroying commercial crops.

← Captive breeding programs for the Rodrigues Flying Fox, that work to ensure genetic diversity exist around the world, are helping to rescue this species from possible extinction.

→ The Greater Mascarene Flying Fox's populations are crashing due to mass culling (killing) ordered by the Mauritian government.

For most other bat species, habitat degradation and loss, global climate change, and urbanization are the most significant threats. Thus, protecting where bats eat and where they sleep are the most important conservation actions for most species. Other conservation threats, typically species-specific, include the medicinal use of bat body parts, particularly in Africa and Asia, and the illegal trade in bat taxidermy. Thousands of bats are killed each year, taxidermied (or simply mummified), imported to the West, and put up for sale on Facebook, eBay, and other commercial sites. Chief among these is the strikingly beautiful Painted Woolly Bat (see page 93), with hundreds of listings on a given day on Etsy of this species, priced as low as US $20. The demand for taxidermied specimens has led to a decline of over 25 percent over the past 15 years. As wild species cannot be "farmed," there is no such thing as "ethically sourced" bat products.

HELPING BATS

With so much bad news for bat populations, what is the path forward? How do we mitigate hunting and the medicinal use of bats, persecution, the effects of habitat loss and degradation, urbanization, global change, and the "oddities" market? How do we protect where bats eat and sleep? Part of the answer lies in education and in transforming the negative perception of bats held by people all over the world. Replacing these negative views of bats with respect and appreciation for them and for the roles they play in global environments will take hard work. A holistic understanding of how bat health, ecosystem health, and human health are intertwined is also critical. Fortunately, the workforce for these efforts is largely in place.

All around the world, regional and global networks serve to connect local stakeholders, researchers, and conservationists. Internationally connected through participation in the Global Union of Bat Diversity Networks (GBatNet), these networks are now actively collaborating to share knowledge, build capacity, help determine the most critical research and conservation efforts, and then to coordinate these efforts in the service of bat conservation. Wish us luck!

↑ Bat caring or rehabilitation can provide a chance at life for orphaned or injured bats, like these Spectacled Flying Fox pups, with the goal of eventual release.

→ Protecting where bats eat and where they sleep, like this pitcher plant that provides a roost for Hardwicke's Woolly Bat (*Kerivoula hardwickii*), will go a long way towards ensuring a future world with bats.

CHALINOLOBUS DWYERI

Large-eared Pied Bat

Rare and particular

SCIENTIFIC NAME	*Chalinolobus dwyeri*
FAMILY	Vespertilionidae
DIET	Insectivorous (no details known)
HABITAT	Rocky areas and surrounding habitat
CONSERVATION STATUS	Vulnerable
WEIGHT	0.19–0.42 oz (5.5–12 g)
WINGSPAN	Not known

The Large-eared Pied Bat is only known from five maternity roosts in fragmented habitat in eastern Australia. Habitat degradation and the increased frequency of wildfires imperils this naturally rare species.

This species earns the large-eared portion of its common name for its comparatively long and broad ears, which are thickened and folded in at the margins. Its tragus is large and curves inward. On its otherwise nearly black pelage, a white band or stripe of fur occurs at the edge between the fur on the front and the wing membranes, earning the pied moniker. Large glands appear at each side of the muzzle—in males during the breeding season, these glands become even more swollen and exude a milky section. Its purpose is unknown, but it likely plays a role in sexual attraction and mating.

Although some bat species are resilient to change and will utilize a broad array of habitat types, others like the Large-eared Pied Bat have very specific requirements for both foraging and roosting. This species is poorly known, but data suggest that it fares best in the sandstone areas of the Central Queensland Sandstone Belt, the Sydney Basin, and Pilliga (in New South Wales, Australia). Mathematical modeling of its distribution indicates that this species requires the specific combination of sandstone (or other rocky substrate) escarpment for roosting and fertile valleys for foraging. This species roosts in cliffs or rocky outcroppings in the twilight zone (areas that receive some light and are not fully dark). It forages in surrounding areas in habitats that include open eucalyptus forest with a rainforest canopy, at the edge of rainforest habitat, dry and wet sclerophyll forests (those adapted for long periods of dry heat) and woodland, and subalpine woodland.

Species that are naturally rare and have very specific requirements are by nature more likely to be threatened with extinction in the face of anthropogenic activities and global change. At least 30 percent of the Large-eared Pied Bat's range burned during wildfires in 2019–2020 alone.

Large, thick ears

The ears of this bat species are especially thick and larger than those of its close relatives.

→ White fur rings the bat body on its ventral side, a distinguishing feature of this small, insect-eating bat.

CRASEONYCTERIS THONGLONGYAI

Hog-nosed Bat

Tiny treasure

SCIENTIFIC NAME	*Craseonycteris thonglongyai*
FAMILY	Craseonycteridae
DIET	Small moths, beetles, and other insects
HABITAT	Limestone caves and nearby forests
CONSERVATION STATUS	Near Threatened
WEIGHT	0.06–0.11 oz (1.7–3.2 g)
WINGSPAN	Not known

The Hog-nosed Bat is a unique and rare species first described in 1974. Its features set it apart from all other Chiroptera, which warranted the establishment of an entirely new bat family, Craseonycteridae, for this tiny bat with a turned-up nose.

This distinctive species was discovered in 1973 by Thai scientist Kitti Thonglongya, who died shortly thereafter. Upon the invitation of the Thai government, his collaborator at the British Museum of Natural History published the formal description of this new species in 1974, naming it for his friend and colleague. It is most closely related to the Megadermatidae (false vampire bats, of which there are six species) and the Rhinopomatidae (mouse-tailed bats, also six species), both also relatively unusual lineages of Old World bats.

Female Hog-nosed Bats give birth to a single pup each year, late in the dry season. These bats have a pair of "false" or inguinal nipples in the pelvic region that serve as attachment points. The pup clings to its mother's front upside down (that is, right side up to us), holding the inguinal nipple in its mouth and using its feet and legs to cling to the mother's neck. The Hog-nosed Bat is an obligate cave rooster that is believed to remain near the roost for life.

Additional populations of the Hog-nosed Bat were later found in Myanmar, but preliminary research suggests that the Myanmar populations may be a different species. The Thai population (around 6,500 bats) is recorded from 44 caves, whereas the Myanmar population (around 3,800 bats) is recorded from nine caves. Additional surveys are required to determine if any other populations of this bat exist. The rarity of this species and disturbance at its roost sites pose significant conservation risks. Unlike losing a bat species from a well-represented genus (like *Myotis* with its 139 species), the loss of the Hog-nosed Bat would represent the loss of an entire unique and ancient bat lineage.

→ The scientific community was amazed at the discovery of this unusual and exceptionally rare bat species, the smallest bat in the world. This individual appears to have mites attached to its ears.

KERIVOULA PICTA

Painted Woolly Bat

Not a good souvenir

SCIENTIFIC NAME	*Kerivoula picta*
FAMILY	Vespertilionidae
DIET	Spiders and some small insects
HABITAT	Dry forests and scrubland
CONSERVATION STATUS	Near Threatened
WEIGHT	0.16–0.19 oz (4.5–5.5 g)
WINGSPAN	7.1–11.8 in (18–30 cm)

The Painted Woolly Bat is one of the most visually striking bats in the world. Its long, dense, and woolly fur ranges in color from light yellow to bright orange to tawny red, with males brighter than females. Wings are orange and black.

The beautiful Painted Woolly Bat is geographically widespread, yet relatively uncommon. It roosts alone or in small monogamous family groups in foliage or under large leaves, preferring dried or dead banana leaves. It has also been found roosting in unusual places, including flowers, dry grass, and weaver bird nests. They are torpid while in these day roosts and thus slow to arouse when disturbed.

In data from Thailand, male and female pairs were found roosting with a single infant in February, June, September, and October, but not in November and December. At this time, young are assumed to have dispersed and only the pair remained. The foraging areas of each pair did not overlap with those of other bats, suggesting that they may be territorial. The Painted Woolly Bat may change partners each breeding season.

Painted Woolly Bats feed mostly on web-building spiders, which they find by foraging low to the ground in bushy and densely vegetated areas. Their flight appears fluttery, like that of a moth, and they are highly maneuverable fliers. Their low-intensity, short-duration, broadband echolocation calls are adapted for cluttered environments and for gleaning their prey. Until recently this species was classified as of Least Concern, but the large demand for taxidermied or mummified specimens and skulls as souvenirs and collectable oddities both online and in physical stores (locally and in foreign countries) has led to precipitous declines.

→ A victim of its own beauty, populations of the unbelievably colorful Painted Woolly Bat are being decimated for the souvenir trade.

PTEROPUS NIGER

Greater Mascarene Flying Fox

Island endemic

SCIENTIFIC NAME	*Pteropus niger*
FAMILY	Pteropodidae
DIET	Native and commercial fruits
HABITAT	Forested mountain ranges
CONSERVATION STATUS	Endangered
WEIGHT	0.16–0.19 oz (4.5–5.5 g)
WINGSPAN	7.1–11.8 in (18–30 cm)

The Greater Mascarene Flying Fox is found on two small islands, Mauritius and Réunion, in the western Indian Ocean, east of Madagascar. Imperiled by both legal and illegal hunting, its classification as an Endangered species may soon be changed to Critically Endangered.

This species roosts in forested mountain ranges but also in forest remnants throughout the island nation of the Republic of Mauritius. The Greater Mascarene Flying Fox may change roosts often and satellite telemetry has shown that bats may travel up to 57 miles (92 km) in a night to forage in forests and in urban settings and orchards. It feeds on fruit and flowers from both native and commercial fruit species, such as mango and lychee.

The Greater Mascarene Flying Fox went extinct on Réunion, a French overseas department, in the early eighteenth century. It likely vanished due to forest clearing and hunting, in a similar way to the Small Mauritian Flying Fox (*Pteropus subniger*) from Réunion and Mauritius, which went extinct in the nineteenth century. However, in 2007 a small colony of approximately 40 Greater Mascarene Flying Foxes was found on Réunion, which either originated from released zoo animals or from storm activity, blown over from Mauritius. It is unclear if this colony is viable in the long term.

The situation in Mauritius is dire, with government-sponsored culls of this protected species facilitated by its reclassification as a pest species. The Special Mobile Force of the Republic of Mauritius shot nearly 31,000 bats in 2015 and over 7,000 bats in 2016, including in protected forests. Pressure from Mauritian and international conservation organizations has resulted in stakeholder dialogues. This has brought a small measure of stability and raises hope for the species.

→ The Greater Mascarene Flying Fox is recognized by its pale face and relatively small ears.

TADARIDA BRASILIENSIS

Brazilian Free-tailed Bat

The fastest flier

SCIENTIFIC NAME	*Tadarida brasiliensis*
FAMILY	Molossidae
DIET	Moths and other flying insects
HABITAT	Variable, including forests, scrub, and deserts
CONSERVATION STATUS	Least Concern
WEIGHT	0.28–0.53 oz (8–15 g)
WINGSPAN	11 in (28 cm)

The Brazilian Free-tailed Bat roosts in caves but also readily adapts to human and urban structures. Widely distributed from North to South America and roosting in massive numbers, this is an exceptionally successful and common species.

The fast-flying Brazilian Free-tailed Bat is very well studied. Well-known and protected colonies occupy roosts throughout their range, from the Congress Avenue Bridge in Austin, Texas, to the attic of the Faculty of Law building at the National University of Rosario in Argentina. The population of Brazilian Free-tailed Bats at Bracken Cave in Texas is estimated at 15 million or more, making it the world's largest bat colony and one of the largest concentrations of mammals on the planet.

Due to the sheer number of bats in some roosts, bats begin exiting their roost well before sunset so as to get far enough away from roostmates to find food. This creates ripe opportunities for predators such as kestrels, kites, hawks, owls, and grackles. These avian predators, along with snakes and a few opportunistic mammals like raccoons, skunks, and opossums, can eat their fill nightly but don't make a significant dent in the bat population.

Numbers of bats within a roost peak each year when females give birth to a single pup. Young bats roost separately from their mothers, at a density of 400 pups per square foot. Since they are hairless, such tight packing keeps pups warm while their mothers are foraging. After 4 to 5 weeks, young attempt their first flight—testing out their echolocation capabilities while trying to avoid collisions with other young fliers. Pups that fail and land on the ground are quickly devoured by the millions of carnivorous dermestid beetles on the cave floor. Less than half of all young Brazilian Free-tailed Bats survive their first year.

→ The Brazilian Free-tailed Bat is one of the few species that spans large portions of both North and South America. Free-tailed bats, like this individual, drop from the roost before taking full flight.

↑ Brazilian Free-tailed Bats leaving a south Texas cave.

BAT FAMILIES

FAMILY (21 IN TOTAL)	NUMBER OF SPECIES	FAMILY COMMON NAME	DISTRIBUTION
Pteropodidae	202	World Fruit Bats	Asia, Australia, Pacific Islands, Africa
Rhinonycteridae	9	Trident Bats	Australia, Africa, Madagascar
Hipposideridae	92	Old World Leaf-nosed Bats	Southeast Asia, Australia, Africa
Rhinolophidae	114	Horseshoe Bats	Southeast Asia, Australia, Eurasia, Africa
Rhinopomatidae	6	Mouse-tailed Bats	Southern Asia, Africa
Megadermatidae	6	False Vampire Bats	Southeast Asia, Australia, Africa
Craseonycteridae	1	Hog-nosed Bats	Southeast Asia
Cistugidae	2	Wing-gland Bats	Southern Africa
Vespertilionidae	533	Vesper Bats	Worldwide (except Arctic and Antarctic regions)
Miniopteridae	41	Bent-winged Bats	Asia, Australia, Eurasia, Africa
Molossidae	135	Free-tailed Bats	Asia, Australia, Americas, Eurasia, Africa
Natalidae	11	Funnel-eared Bats	Tropical Americas
Mystacinidae	2	New Zealand Short-tailed Bats	New Zealand
Thyropteridae	5	New World Disk-winged Bats	Tropical Americas
Furipteridae	2	Smoky Bats	Tropical Americas
Noctilionidae	2	Bulldog Bats	Caribbean Islands, Tropical Americas
Mormoopidae	18	Mustached Bats	Caribbean Islands, Tropical Americas
Phyllostomidae	230	New World Leaf-nosed Bats	Caribbean Islands, Tropical Americas
Myzopodidae	2	Old World Disk-winged Bats	Madagascar
Nycteridae	14	Slit-faced Bats	Southeast Asia, Africa
Emballonuridae	55	Sheath-tailed Bats	Pantropical: Southeast Asia, Australia, Africa, Tropical Americas

GLOSSARY

airfoil A curved cross-sectional portion of a wing that produces upward aerodynamic force (lift).

aposematism A display that warns predators that an animal is unpalatable, toxic, venomous, or otherwise dangerous.

Batesian mimicry A display in a non-threatening species that resembles that of an aposematic species; invoking the same predator avoidance.

boreal A reference to being located in northern regions.

calcar A small spur of cartilage that arises from the ankle and helps support the uropatagium; present in most species of bats.

Coleoptera The order of insects composed of all beetles; with over 400,000 species, it constitutes 25 percent of all known animal species.

countershading A form of camouflage in which an animal's coloration is darker on the back and lighter on the underside.

dactylopatagium The portion of the bat wing membrane that stretches between the digits, or fingers.

Diptera The order of insects composed of all flies and their close relatives, including mosquitos.

duty cycle A metric applied to sounds made periodically (like echolocation calls), calculated as the proportion of time spent emitting a sound.

echolocation A sensory system in which an animal emits a sound and interprets the returning echoes of that sound; bats also use navigation to hunt prey.

ectothermy A temperature regulation strategy in which animals rely on external heat sources to increase their body temperature.

endothermy A temperature regulation strategy in which animals can generate their own body heat through internal physiological processes.

hawking A hunting strategy in which flying prey are captured by flying predators.

heterothermy A temperature regulation strategy in which animals display variable body temperatures; many bat species are heterothermic endotherms.

hibernaculum (pl. hibernacula) A typically cold location in which animals hibernate, roosting for prolonged periods of time in torpor.

homeothermy A temperature regulation strategy in which animals display near constant body temperatures.

hyperphagic A state in which an animal eats significantly more than usual.

keel An anatomical process forming a ridge or projection, provides additional surface area for muscle attachment.

Lepidoptera The order of winged insects that includes butterflies and moths. Second largest order of insects behind Coleoptera.

littoral An area of water close to the shore, sometimes called nearshore.

mesic A habitat type in which a moderate supply of moisture is present, especially during seasonal growing periods.

montane A type of ecosystem found along the slopes of mountains; as elevation increases, habitat types can change dramatically; biodiversity is high.

neotropical Pertaining to the biogeographic realm that includes tropical terrestrial ecoregions of North and Central America and all of South America.

niche The ecological role of an organism in a community; includes diet, habitat use, and interactions with other species.

niche partitioning The process by which competing species use the environment differently, for example by choosing different roosts or prey, which helps them coexist.

obligate A term that describes a necessary and essential process for survival.

Orthoptera The order of insects containing grasshoppers, locusts, and crickets and their close relatives.

patagium All of the sections of skin that form the bat wing; stretched across the bony fingers, they allow bats to fly.

pelage The total body covering of fur of an animal.

phenotype The observable traits or characteristics of an organism, such as size, color, shape, behavior; arise from gene and environment interactions.

plagiopatagium The portion of the bat wing membrane that stretches between the forearm, the fifth digit, the bat's side, and the bat's ankle.

propatagium The portion of the bat wing membrane anterior to the forearm, connecting the wrist to the bat's shoulder.

reticulated Having an appearance resembling a net or network with veins, fibers, or lines crossing.

riparian A habitat along the edge of a river or stream.

rostrum A forward extension of the face in front of the eyes and containing the nose and mouth; can be exceptionally long in some nectivorous bats.

sexual dimorphism The presence of different morphological traits in males and females of the same species.

synanthrope An organism that lives near and benefits from humans and human-made environmental modifications.

thermoconforming The alignment of body temperature with environmental temperature; the opposite of thermoregulation.

thermoregulation The maintenance of body temperature through behavior and physiological mechanisms.

torpor A state of depressed metabolism, typically at low body temperature; can be short-lived or last for days to weeks.

tragus A piece of skin in front of the ear canal that directs sounds into the ear and aids in echolocation; most bat species have one.

ulnar sesamoid A bone that is associated with the tendons of the elbow and that may support flight; within mammals only found in bats.

uropatagium The wing membrane found between a bat's hind legs; not present in all species.

volancy The ability to truly fly, in contrast to gliding.

xeric A relatively dry habitat type in which a little water is present; includes deserts and shrublands.

↓ Gray Long-eared Bat

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BAT ORGANIZATIONS

Bat Conservation International
www.batcon.org

Global Union of Bat Diversity Networks
www.gbatnet.org

Global South Bats
www.globalsouthbats.org

The Bat Specialist Group of the World Conservation Union (IUCN)'s Species Survival Commission (BSG)
www.iucnbsg.org

IUCN Red List of Threated Species
iucn.redlist.org

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